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Classification of Peatlands for Forest Drainage and Growth :

A Pilot Study in North-Central Alberta

by



Kerttu Härkönen

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Forest Science

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THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Classification of Peatlands for Forest Drainage and Growth : A Pilot Study in North-Central Alberta submitted by Kerttu Härkönen in partial fulfilment of the requirements for the degree of Master of Science.

*To my friends,
Canadian, Finnish and all the others,
for the unforgettable times shared in the U of A*

Abstract

In a pilot study of peatland classification for forestry purposes, three forested peatland areas in the Lesser Slave Forest Area in north-central Alberta were examined.

Vegetation was described from 131 systematically established sample sites. Relationships between the vegetation cover and the water and peat properties on the sites were studied by subsampling for water and peat on about half of the sites. These samples were analyzed for properties important for forest growth. The vegetation data were classified using a two-way indicator species analysis, TWINSpan, which resulted in 3-8 vegetation groups. The validity of these groups to reflect the differences between sites in forest growth potential was studied by comparing their water and peat properties statistically.

The areas were transitional rich fens. Median values for surface water pH on the two main study areas were, respectively, 6.66 (range 4.10-7.22, n=38) and 6.98 (6.57-7.53, n=13), and mean electric conductivity values 111 ± 38.4 (n=36) and 200 ± 38.9 (n=13) μS . In spite of the uniformity of the data, vegetation groups that can be called deficient in their peat nutrients for sustained forest growth, most importantly total nitrogen and phosphorus, could be distinguished. They were characterized by ombro- or oligotrophic indicator species Sphagnum fuscum (Schimp.) Klinggr., Hylocomium splendens (Hedw.) BSG, Pleurozium schreberi Brid. Mitt., Ledum groenlandicum Oeder and

Vaccinium vitis-idaea L. Their total peat nitrogen values were under 1.3 %, which in the literature is cited as the minimum value for sustained forest growth, and also their peat phosphorus values bordered on insufficiency. Forest cover on these sites was dominantly Picea mariana (Mill.) BSP. Vegetation groups that had sufficient soil nutrients for sustained forest growth were denoted by meso-eutrophic indicators Carex aquatilis Wahlenb., Brachythecium turgidum (C. J. Hartm.) Kindb., Plagiomnium ellipticum (Brid.) Kop., Sphagnum warnstorffii Russ. and Tomenthypnum nitens (Hedw.) Loeske, and had either a pure Larix laricina (Du Roi) K. Koch or Picea mariana - Larix laricina forest cover.

Vegetation data were also analyzed by a detrended correspondence analysis DECORANA. An interpretation of the resulting ordination was obtained by correlating the samples site scores on the first two axes with the environmental parameters of the sites. The results supported those acquired by TWINSpan.

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Table of Contents

Chapter	Page
I. Introduction	1
A. Object of interest: peatlands	1
B. Peatlands in Alberta	5
C. A Classification/Utilization Case: Finland	9
D. Study objectives	11
II. Methods	13
A. Study areas	13
B. Sampling	15
C. Water, peat and vegetation analyses	18
III. Results and discussion	24
A. Characterization of the study areas	24
B. TWINSPAN-analyses, all sites	27
NOTREES data set	27
BASAL data set	36
C. TWINSPAN-analyses, Area I	42
NOTREES data set	42
BASAL data set	47
D. TWINSPAN-analysis, Area II, both data sets	52
E. Indicator species considerations	56
F. DECORANA- analyses	57
G. Water table depth and hydraulic conductivity ...	66
H. Peat fibre content	68
I. Peat depth	68
J. Peat chemistry	69
pH	69

Nitrogen	70
Phosphorus	73
Potassium	75
Exchange capacities and calcium content	76
IV. Conclusions	78
V. References	83
VI. Appendices 1-7	97

List of Tables

Table	Description	Page
1.	Average tree growth on peatlands in southern Finland.....	12
2.	Means and standard deviations of important water and peat properties (median values and ranges for water and peat pH) and tree cover on the three study areas.....	25
3a.	Means and standard deviations of important water and peat properties and tree cover of the TWINSPAN-vegetation groups; all sites, NOTREES data set.....	33
3b.	The significant differences among the vegetation groups of the TWINSPAN- analysis for all plots, NOTREES data set.....	35
4a.	Means and standard deviations of important water and peat properties and tree cover of the TWINSPAN-vegetation groups; all sites, BASAL data set.....	40
4b.	The significant differences among the vegetation groups of the TWINSPAN- analysis for all plots, BASAL data set.....	41
5a.	Means and standard deviations of important water and peat properties and tree cover of the TWINSPAN-vegetation groups; Area I, NOTREES data set.....	45
5b.	The significant differences among the vegetation groups of the TWINSPAN- analysis for Area I, NOTREES data set.....	46
6a.	Means and standard deviations of important water and peat properties and tree cover of the TWINSPAN-vegetation groups; Area I, BASAL data set.....	50
6b.	The significant differences among the vegetation groups of the TWINSPAN- analysis for Area I, BASAL data set.....	51

7a.	Means and standard deviations of important water and peat properties and tree cover of the TIWNSPAN-vegetation groups; Area II, both data sets.....	55
7b.	The significant differences among the vegetation groups of the TWINSKAN-analysis for Area II, both data sets.....	55

List of Figures

Figure	Description	Page
1.	Locations of the study areas: Area I at Saulteaux River (1), Area II at Athabasca Highway (2) and Area III at Lesser Slave River (3).....	14
2.	TWINSPAN-analysis for all sites with the NOTREES data set; the indicator species and the number of sample sites of vegetation groups 1-8.....	29
3.	TWINSPAN-analysis for all sites with the BASAL data set; the indicator species and the number of sample sites of vegetation groups 1-8.....	37
4.	TWINSPAN-analysis for Area I with the NOTREES data set; the indicator species and the number of sample sites of vegetation groups 1-8.....	43
5.	TWINSPAN-analysis for Area I with the BASAL data set; the indicator species and the number of sample sites of vegetation groups 1-7.....	48
6.	TWINSPAN-analysis for Area II with both data sets; the indicator species and the number of sample sites of vegetation groups 1-3.....	54
7.	The sample sites plotted according to their scores on the first two axes of the DECORANA-analysis; all sites, NOTREES data set. The corresponding TWINSPAN-vegetation groups superimposed on the scattergram.....	59
8.	The sample sites plotted according to their scores on the first two axes of the DECORANA-analysis; Area I, NOTREES data set. The corresponding TWINSPAN-vegetation groups superimposed on the scattergram.....	61
9a-b.	Correlations between the first axis DECORANA- scores of the TWINSPAN-vegetation groups and their water pH (a) and black spruce and tamarack basal area values (b), Area I.....	62

9c-d.	Correlations between the first axis DECORANA-scores of the TWINSpan-vegetation groups and their total peat nitrogen (c) and phosphorus (d) values, Area I.....	63
10.	The sample sites plotted according to their scores on the first two axes of the DECORANA-analysis; Area II, NOTREES data set. The corresponding TWINSpan-vegetation groups superimposed on the scattergram.....	65

List of Photographs

Photograph	Description	Page
1-2.	Lichen-covered black spruce - tamarack -forest on study Area I in late spring (1) and in July (2).....	28
3.	Black spruce - <u>Ledum</u> - <u>Pleurozium</u> -site on Area III, representing vegetation group 3 in Figures 2 and 3.....	31
4.	<u>Pleurozium schreberi</u> covering forest floor on a dry site.....	31
5-6.	Tamarack -sites on Area I with abundant understory vegetation (vegetation group 5 in Figures 4 and 5).....	39
7.	<u>Plagiomnium ellipticum</u> , an important indicator species in the TWINSPAN -analyses...	41
8.	<u>Sphagnum warnstorffii</u> , the most commonly occurring Sphagnum -species on Area I.....	51
9.	<u>Sphagnum fuscum</u> - (left) and <u>Tomenthypnum</u> <u>nitens</u> (right) -hummocks on Area II	53
10.	Three typical moss species from Area II: <u>Sphagnum angustifolium</u> (upper left corner), <u>Sphagnum warnstorffii</u> (middle) and <u>Tomenthypnum</u> <u>nitens</u> (to the right).....	53

I. Introduction

A. Object of interest: peatlands

Peatlands cover vast areas in Canada and there is a growing interest in their use and management. Peatlands are a part of wetlands, which, by the Canadian definition, are areas where wet soils are prevalent with a water table near or above the mineral soil and which support hydrophilic vegetation. Wetlands include areas other than peatlands (e.g. shallow open water, marshes). The area covered by wetlands in Canada is estimated to be 170×10^6 ha, or 18 % of Canada's land surface (Zoltai and Pollett 1983).

Peatlands are unbalanced systems where the production of organic matter exceeds the rate of respiration and decomposition. This is caused by excess water on the site and results in an accumulation of peat. Peatlands develop where water is temporarily stored or collected on its way from the catchment to the sea (Moore and Bellamy 1974). For a peatland to originate, evaporation and evapotranspiration must be less than precipitation, and the climate must not be too extreme so that biomass can be produced. Thus, the most favourable areas for peatland formation are areas with cool, moist climates with expanses of flat terrain. They occur in temperate, boreal and subarctic zones in the northern hemisphere, and in more limited areas in the southern hemisphere (Kivinen and Pakarinen 1981). A good example is the Hudson Bay Lowlands, the most extensive contiguous

wetland in Canada (Zoltai *et al.* 1973) and one of the greatest concentrations of peatlands found in the boreal zone (Sjörs 1961). The total area of peatlands in Canada is estimated to be 150×10^6 ha or 16% of Canada's land surface (Kivinen and Pakarinen 1981).

Peatlands develop in several different ways. Firstly, primary peatland formation occurs when the colonizing vegetation on a site are peatland species, which can modify site conditions to be unfavourable for other kind of vegetation. Secondly, forest land can turn into peatland by paludification, when the water balance on a site is changed, e.g. due to damming, or when surface and subsurface flow of water is very low. Thirdly, filling up of ponds and lakes with hydrophilic vegetation also produces peatlands. In Canada, wetland development is relatively youthful, following deglaciation 7000 - 14000 years ago, drainage of glacial lakes and the emergence of land from the sea (Zoltai and Pollett 1983).

Peatlands can be defined in biological and geological terms. Biologically, a peatland is a peat forming plant community, accumulating *in situ*. Geologically, peatlands are areas with peat deposits (Cajander 1913). The depth of the deposit required to classify the area as peatland varies. In Germany, it is 20 cm (Schneider 1976), in Ireland 45 cm (Hammond 1979); and in the Nordic countries, as well as in recent statistics of IUFRO, the International Union of Forest Research Organizations, (Haverlaen 1977) and IPS, the

International Peat Society (Kivinen 1980) it is 30 cm. In the System of Soil Classification for Canada, peat thickness required for organic soils (peatlands) varies from 40 cm for medium- or well-decomposed peats (Rennie 1977) to 60 cm for weakly decomposed fibric peats (Kivinen and Pakarinen 1981).

In this thesis, the word 'peatland' is used as the general term for the areas under study. The terminology in peatland research is highly variable. General peatland terms include 'mire', an English word used for undrained peatlands with peat-forming vegetation; 'muskeg', a Canadian Indian word, originally meaning an area more or less covered with Sphagnum-mosses, sedges and an open growth of scrubby timber; 'organic terrain' - all meaning approximately the same thing (Stanek 1977a).

Other terms pertaining to wetlands are e.g. bog, fen, carr, marsh, swamp (Jeglum *et al.* 1974). From these, 'bog' and 'fen' are most frequently used in differentiating peatland types. The differences between peatland types are based on the hydrologic balance of a basin and the amounts of minerals in the solution (Moore and Bellamy 1974). Separation between bogs and fens is based on the origin of peatland waters, a system developed to its present form mainly by Swedish scientists (DuRietz 1949, 1954; Sjörs 1948, 1950, 1952).

Bogs are areas where only precipitation is directly influencing the living vegetation. Bogs are separate from regional groundwater systems and are characterized by water

with low pH and low ion concentrations and scarce nutrient availability for plants. The nutrient content of water and peat, theoretically, cannot exceed those of precipitation, as their vegetation is the result of peat accumulation over and above mire waters that are in contact with mineral soils. Bogs are frequently described as being ombrotrophic, a definition first used by DuRietz (1954). The classic German term for these areas is *Hochmoore*, and also terms such as 'ombrogenous mires' (von Post and Granlund 1926) and 'ombrophilous peat-bogs' (Kulczynski 1949) have been used.

On the other hand, fens are peatlands where the primary means of recharge is from the local or regional groundwater system. These areas are called minerotrophic. Minerotrophy is usually indicated by high values of pH, Ca^{2+} , Mg^{2+} and electric conductivity of the mire waters. The suggested lower limit for minerotrophy is pH=4.0 (Boelter and Verry 1977) or pH=4.2 (Sjörs 1952). Also this term, as opposed to ombrotrophic, was first used by DuRietz (1954). Earlier references to these areas have been *Niedermoore* (as opposed to *Hochmoore*), 'topogenic' and 'soligenic' mire (von Post and Granlund 1926), 'mineral soil water mire' (Ackenheil 1944), 'rheophilous peat-bog' (Kulczynski 1949), 'limnogenic' and 'geogenic' mire (Sjörs 1948). A series from poor through transitory and intermediate to rich fens can be distinguished on the basis of pH and ion concentrations of the mire waters, and indicator species can be identified to separate these (Sjörs 1950, 1961, 1963).

Another direction of variation in peatlands is the trophic gradient, which is used to describe the fertility of peat. The trophic gradient is positively correlated with the concentrations of major cations (calcium, magnesium) and with the pH and electric conductivity of surface peat and mire waters. Also the contents of total nitrogen in peat reflect the trophic status, while trends for total phosphorus and potassium are more diffuse (Heikurainen 1979, 1982). The trophic series ranges from oligotrophy through mesotrophy to eutrophy with increasing fertility. To describe the nutrient status of peat, the phosphorus and potassium values have to be considered in addition to the trophic status.

B. Peatlands in Alberta

Geographical differences in temperature and annual precipitation bring about a great variability in peatlands. As a peatland develops, the importance of local topography and nutrient supply decreases, and the character of peatlands and their regionality reflect changes in macroclimatic conditions, such as the temperature regime and the oceanity-continentality -aspect of the area. These patterns have been described for eastern North America by Damman (1979) and for Europe by Moore and Bellamy (1974). In the Canadian wetland classification, which began in the 1970's (Zoltai *et al.* 1973), it was necessary to separate different regions, along a north-south temperature gradient

and an east-west precipitation gradient. Sixteen regions were recognized, in six major zones (Zoltai and Pollett 1983).

In the province of Alberta, four of these zones are represented. The south-eastern part of the province belongs to the Grassland Prairie Wetland District, with no peatland development. The wetlands are wet meadows and fresh to saline marshes in depressions, containing semi-permanent shallow lakes. The wetlands in the Rocky Mountains represent the Mountain Complex, occurring only in the valleys and on lower slopes. Most of the province is part of the Continental Mid-Boreal Wetland District, characterized by cold winters and hot summers with low amounts of precipitation. Permafrost does not occur in the region. Flat bogs and basin bogs occur associated with fens. Occasionally, somewhat elevated flat-topped bog plateaux occur in fens, often separated by patterned fens. ('Bog' as used here by Zoltai¹, refers to Sphagnum-dominated vegetation and even small patches of S. fuscum. are so called.) The northern part of the province is part of the High Boreal Wetland Region. The climate is characterized by cold winters and moderately cool summers, with low precipitation. The wetlands are typically patterned fens (ribbed and netted), small wooded peat plateaux and palsas, and flat bogs and fens (Zoltai and Pollett 1983).

¹ Personal communication: Discussion, Feb. 1985

Generally, in the southern third of the province, wetlands occupy less than 5 % of the total land surface. In the boreal zone, the proportion is much higher. According to Slack *et al.* (1980), 25 - 33% of the forested area of Alberta is covered by peatland of one sort or another. This area is estimated to be at least 800 000 ha (Korpijaakko and Woolnough 1977), probably much more. These peatlands were studied in the 1920's by Lewis and Dowding (1926) and Lewis *et al.* (1928), followed by Moss (1953), Radforth (1958) and Moss and Pegg (1963). More recent work was done by Vitt (1973), Vitt *et al.* (1975), Vitt and Andrus (1977), Horton *et al.* (1979) and Slack *et al.* (1980). The general picture emerging from these studies is that of extensive fens, with truly ombrotrophic conditions being present only in microhabitat situations (sometimes in complexes called mixed mires, which are evidently called bog-fen associations in Zoltai and Pollett 1983). The fens are conspicuous owing to the continental climate and the absence of permafrost, and their high ionic values are the result of calcareous bedrock and groundwater. In some areas in northern Alberta, the occurrence of permafrost has led to the development of more or less ombrotrophic landscapes (Horton *et al.* 1979).

The studies of peatlands of Alberta have so far been mainly botanical, comparing Alberta's peatlands with those in northern Europe. According to Sjörs (1959) and Slack *et al.* (1980), there is much similarity between Fennoscandian and Canadian boreal and subarctic vegetation. The similar

species occur notably in the bryophyte layer, with less similarity in the vascular plant species. Several of the indicator species for different types of Fennoscandian peatlands can also be used to characterize peatlands in Alberta.

These studies have laid the basis for further peatland work in Alberta. One direction is the investigation of the utilization of these areas for forestry. The forests on organic soils in Alberta occur mainly in Mixedwood (B18a), Hay River (B18b) and Upper Mackenzie (B23a) Forest Sections (Rowe 1972). These areas are forested to an extent of 75 % of the total land area (Rennie 1977) . They are occupied dominantly by black spruce (Picea mariana (Mill.)BSP) and to a lesser extent by tamarack (Larix laricina (Du Roi)K.Koch). The commercial utilization of these sites has been slight; however, their importance for forestry is expected to grow in the future, due to their large area, a decreasing land base in forestry and an increasing demand for renewable resources. Considering the success reported in managing peatlands for forestry in Fennoscandia and the USSR, there is interest into the potential of the same in Alberta (Hillman 1984).

Operations required in reclaiming peatlands for forestry are drainage and possibly fertilization. A site classification needs to be drawn up to form the basis for decisions on how to make peatlands more productive for forestry, and to judge which sites are suitable for forest

growth.

C. A Classification/Utilization Case: Finland

The peatland classification system used in Finland can be presented as an example of a classification for forestry purposes. Finland is a country with 30 % of its land area, 10.4×10^6 ha, covered with peatlands, and an extensive program in utilizing these lands for forestry.

Studies in peatlands in Finland date from the 1870's (Norrlin 1871, Wainio 1878). The classic peatland classification work is by Cajander from 1913. In this work, 'Studien über die Moore Finnlands', Cajander described the major categories of the Finnish peatlands, which still today form the basis for classification in both purely botanical and applied studies. The botanical work is represented by Kujala (1921), Kotilainen (1927, 1951), Waren (1926), Paasio (1933, 1941), and Tuomikoski (1942), as well as by studies on the regionality of peatlands by Heikurainen (1953), Ruuhijärvi (1960, 1982), Havas (1961) and Eurola (1962). In the most recent work on these lines, up to 80 site types have been described (Eurola and Kaakinen 1978). For applied, practical purposes, mainly for site evaluation for forestry, 25-35 types are usually distinguished. These sites have been described in field books and guides by Kivinen (1948), Lukkala and Kotilainen (1951), Huikari (1952) and Heikurainen (1960, 1978).

The main idea in Cajander's classification was that of a distinct plant community, a site-type, resulting from competition and reflecting the combination of environmental factors on a site (Cajander 1925). Cajander divided peatland vegetation into main categories on the basis of the dominant tree species. These categories are, in Heikurainen and Pakarinen's (1982) terminology, hardwood-spruce mires, pine mires and treeless mires. In later botanical work, three other ecologically distinct groups (melt water mires, spring mires and swamps), as well as the ecological attributes of each group were described (Eurola and Kaakinen 1978, 1979). Thus, Cajander's Bruchmoore - hardwood-spruce mires, korvet in Finnish, are characterized by shallow peat and meso-eutrophic shade-tolerant hummock vegetation. The best indicator of this class is Norway spruce (Picea abies (L.)Karst.). Cajander's Reisermoores - pine mires, rämeet in Finnish, are characterized by ombro- or oligotrophic hummock vegetation. Scots pine (Pinus sylvestris L.) and dwarf shrubs are the best indicators. Treeless mires are divided into two groups. Weissmoore - poor fens/bog hollows, nevat in Finnish, are characterized by ombro- and minerotrophic, oligo- or mesotrophic lawn- and flark-level vegetation and are treeless. Braunmoore -rich fens, letot in Finnish, are treeless peatlands with eutrophic lawn- and flark-vegetation. For practical purposes, the same can be presented as follows: korvet are peatlands characterized by spruce and hardwoods. Rämeet grow pine and dwarf shrubs. In

treeless peatlands, nevat and letot are distinguished on the basis of presence or absence of rich fen species. Cajander's physiognomic divisions, based on the dominant tree species, are still valid and modern research has been able to explain many of the underlying ecological factors that are manifested in these main classes. The plant sociological site classification has been found to reflect the average fertility of surface peat in the virgin state satisfactorily (Westman 1981).

Table 1 (Huikari 1974) gives an example of the classification for forest drainage. Peatland types are presented in six site quality classes, in a continuum from nutrient rich to nutrient poor types, reflecting mainly the contents of peat nitrogen, phosphorus and calcium. The response to drainage diminishes when moving from rich to poor sites. Site quality classes I-IV are considered suitable for drainage in southern Finland.

D. Study objectives

This study was a pilot study on the classification of forested peatlands in Alberta for forest drainage and growth potential purposes. The approach taken was that of a vegetation-based classification. The primary hypothesis was that there are relationships between the vegetation growing on a site and the peat and water qualities of the site important for drainage and forest growth. The objective of this study was to describe and distinguish plant

communities, compare peat and water qualities in these communities and identify relevant relationships. It was further hypothesized that these communities could be distinguished by indicator species, and that they would be indicative of forest growth after drainage, so that they could be used for classifying peatlands for drainage and growth.

Table 1. Average tree growth on peatlands in southern Finland. (Huikari 1974)

Site quality class	Peatland type	Annual increment, m ² /ha	
		Undrained	Drained (50 m spacing)
I	Eutrophic spruce swamps	3.0-0.1	8.0-5.0
	" pine swamps	1.0-0.2	6.0-3.5
	" open peatlands	-	5.0-
II	Forb-rich spruce swamps	1.0-0.5	8.0
	" pine swamps	0.5	7.0-6.0
	" open peatlands	-	6.0-
III	Tall-sedge-Myrtillus-rich spruce swamps	2.0-0.5	7.0-5.0
	" pine swamps	0.5	5.0
	" open peatlands	-	4.0-
IV	Low-sedge-Vitis-idaea-rich spruce swamps	2.5-0.5	4.5-4.0
	" pine swamps	0.5	4.0-2.0
	" open peatlands	-	2.0
V	Cottongrass spruce swamps	0.5	3.5
	" pine swamps	1.0-0.5	3.0-2.0
	" open peatlands	-	1.5
VI	Fuscum pine swamps	0.2	1.0
	" open peatlands	-	0.5-

II. Methods

A. Study areas

The study areas were selected in the vicinity of Lesser Slave Lake, north central Alberta. Three different areas were chosen to obtain a wide range of plant communities and site conditions (Figure 1). The criteria used in the selection were that the areas be forested and differ in their tree cover. The areas also had to be accessible from the road. Selection was based on a study of aerial photographs and on-site reconnaissances. The areas were (1) by the Saulsteaux River (55°09' N, 114°15' W), (2) near the junction of provincial highways 2 and 44 (55°01' N, 114°01' W) and (3) by the Lesser Slave River (55°17' N, 114°24' W). The primary foci of the study were on areas I and II. Area III was less important because of its heterogeneity: part of the area had burned during the last 20 years, a central part of it was open willow thicket, and there were numerous mineral soil sites within it occupied by white spruce (Picea glauca (Moench) Voss).

Physiographically these areas belong to the Lesser Slave Lowlands, with altitudes of 300-600 m a.s.l (Atlas of Alberta 1969). The bedrock on areas I and III is part of the marine Upper Cretaceous Lea Park formation, which consists of shale and glauconitic silty shale (Vogwill 1978). On area II the bedrock is part of the continental Upper Cretaceous Belly River formation, consisting of grey sandstone, grey

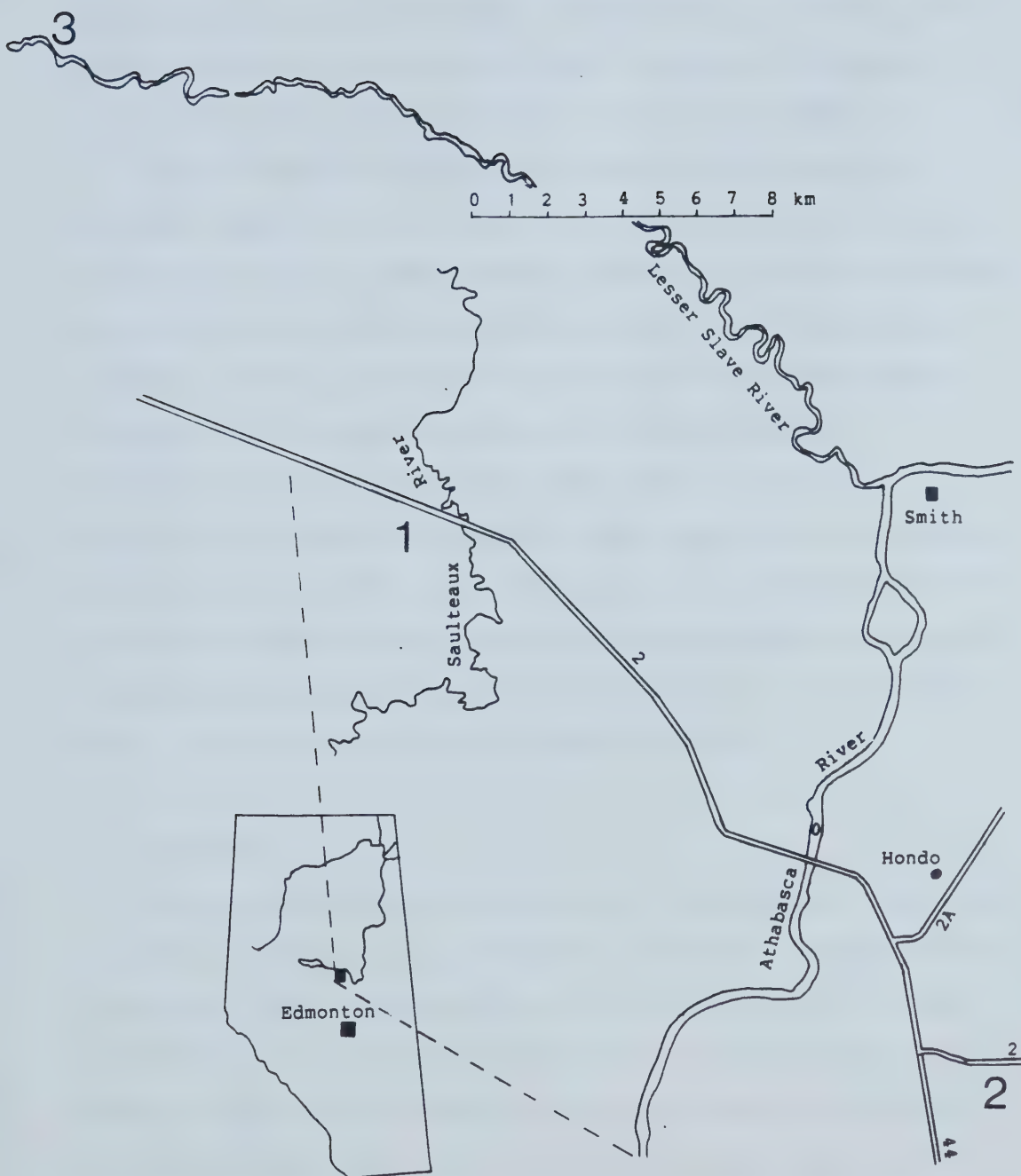


Figure 1. Locations of the study areas: Area I at Saulteaux River (1), Area II at Athabasca Highway (2) and Area III at Lesser Slave River (3).

shale and sandy shale (Campbell 1972). The prevailing soil types on these areas are grey wooded soils, with which the organic soils are associated. Forested organic soils cover about 70% in the vicinity of areas I and III and about 25% in the vicinity of area II (Atlas of Alberta 1969).

The climate on the area is boreal cold temperate (climate type VIII in Walter and Leith 1960), with cold winters and short, cool summers. Annual precipitation varies between 457 mm in the lowlands and 559 mm at higher areas (Vogwill 1978). In 1931-60, appr. 55% of the mean annual precipitation occurred during the growing season (April-August). Slightly less than 30% of the annual precipitation occurred as snow. Mean temperature in January between 1931 and 1960 was -16°C and in July 1931-1960 16.5°C (Atlas of Alberta 1969). Annual potential evapotranspiration (Thornthwaite method) varies from 508 mm in the lowlands to 406 - 457 mm in the uplands (Vogwill 1978).

B. Sampling

A preliminary stratification of the areas by tree cover was done on the aerial photographs. Sampling was designed on the photos with the objective of covering as much of the variability observed as possible. On the three areas, 131 sample sites were systematically established on parallel transect lines, with 150 m distance between plots and 300 m distance between lines, with a random starting point. Seventy-one of the sites were on area I, thirty-nine on area

II and twenty-one on area III. On each site, the ground vegetation was described using 2-4 randomly placed circular plots, 0.25 m² in area. The cover of each species was visually estimated on a scale of 1-10 (10=100% cover, 9=90% cover, etc.), and a '+'- value was given for species covering less than 10% of the plot. Vascular plant layer and bryophyte layer were estimated separately. Unknown species were taken to the laboratory and identified later. A list of the species that occurred on the plots is in Appendix 7. Concurrently, tree cover was described by establishing a 0.01 ha circular plot at each site. All trees exceeding 5 cm in diameter were identified by species and measured for diameter at breast height and total height. On the average, every third tree was cored for growth measurements.² After the initial vegetation sampling was completed, a subsample of 60 sites was taken to define peat and water quality characteristics. These sites were chosen by stratifying the total data set into four physiognomically different classes: black spruce or tamarack dominated, 75-100 % of either species in the basal area, or mixed stands with either black spruce or tamarack having 50-75 % in the basal area. In these four groups, lower vegetation was used as a divisive factor to further separate the groups, with the indicators of the oligotrophy - eutrophy gradient (Heikurainen 1971a, Eurola and Kaakinen 1978, Horton *et al.* 1979). Indicators

²The results of the tree study are presented in a M.Sc.-thesis by A. Mäkitalo, 1985, Dept. Forest Science, University of Alberta.

used for oligotrophy were e.g. Sphagnum fuscum (Schimp.) Klinggr., S. nemoreum Scop., Vaccinium oxycoccos L. and Ledum groenlandicum Oeder; those used for meso-eutrophy were e.g. S. warnstorffii Russ., Tomenthypnum nitens (Hedw.) Loeske and so-called 'brown mosses' as Drepanocladus spp. and Calliergon spp.. Allocation of samples within each group was based on their relative frequency. The subsample size of 60 was determined by the availability of time and resources for further analyses, and the subsampling was carried out in late summer and early fall (Aug. 11-22 and two weekends in October). Peat samples were taken from the upper 30 cm with a core sampler (Holowaychuk *et al.* 1979). Samples were frozen and stored for analysis. Peat depth at each site visited on the second round was also recorded.

Field pH and electric conductivity of the groundwater were measured from natural depressions or other open water holes at each site. A one liter water sample was taken at each site, where possible, for further analysis. At some sites surface water was not available for sampling. Plastic bottles which were rinsed with water from the site were used.

Thirty-one of the sites were later visited for saturated hydraulic conductivity measurements (Boersma 1965). Values for conductivity on Area II were not obtained because water table was mostly below peat in mineral soil; thus the results are presented only for Area I.

C. Water, peat and vegetation analyses

Water samples were analyzed by the Alberta Research Council Chemistry Laboratory for the following:

pH, electric conductivity - standard meters

Ca²⁺, Mg²⁺, Na⁺, K⁺ - optical emission
spectrometer

Peat samples were prepared for analysis by grinding with the equipment of the Soil Science Department, University of Alberta and analyzed by their Laboratory for the following:

pH - in distilled water

(Peat Testing Manual 1979)

total C - dry combustion

(Soil Sci. Am. Proc. 34, pp. 608-610)

total N - Kjehldahl method

extractable N

NH₄⁺ - Industrial Method 98-70W, Oct. 1973

NO₃⁻ - Industrial Method 487-77A, June 1977

total P - Industrial Method 369-75A/A, Nov. 1975

and 334-74W/B, March 1977

extractable P (PO₄⁻) - Bray P1-method

cation exchange capacity and

exchangable cations

NH₄OAc at pH 7

total exchange capacity

- displacement and determination

of adsorbed NH₄⁺

ash - ignition at 550°C

(Peat Testing Manual 1979)

The unrubbed fibre content was determined for 15 peat samples with a method described in the Peat Testing Manual (1979).

The species cover values at each sample site were arithmetically averaged of the 2-4 vegetation plots, yielding one set of values ranging between 0-10 for each site. Two different data sets were used in the analysis: BASAL, where black spruce, tamarack and white spruce included by their basal areas on each sample site, and NOTREES, where the tree species were excluded from the analysis. The results from these two data sets were compared with each other to determine the relationship between lower vegetation and tree cover, and to assess the value of tree species as indicators.

Programs from the Cornell Ecological Package were used to analyze these data. A FORTRAN program called TWINSPAN (Hill 1979b) was used in the classification. TWINSPAN, a two-way indicator species analysis, is a polythetic divisive method of classification. Its basic activity is to make a dichotomy. First the vegetation data are ordinated, or a direction of variation is identified by reciprocal averaging (RA)(Hill 1973). The ordination is then divided in the middle to obtain an initial crude dichotomy. Then, differential species that are preferential to each side of the dichotomy are identified. A 'refined' ordination is then

constructed from the primary one, using the differential species as a basis. Finally, the 'indicator' ordination is constructed based on a few of the most preferential species. There is a method in the program which allows quantitative values to be used as differential 'species' and as indicators. These values are called 'pseudospecies' and they reflect a particular scale of species abundance. The default values for pseudospecies 'cut levels' are 0, 2, 5 and 10. These default values were used in this analysis, as they corresponded with the range 0-10 used for species cover estimations. As an example, it is possible to have a differential species Sph. warnstorffii2, when this species has a coverage value of 2 or greater (the maximum for the bryophyte layer on a given site being 10). The program continues the dichotomous divisions of the data set down to a certain level, the default being six levels. For these data, four levels were defined, and the final units are referred to as 'vegetation groups'.

TWINSPAN offers a variety of options for the user, making it possible to shape the program according to the specifics of the data set. The user has options in several steps of the program. The cut levels of the pseudospecies used in the analysis can be selected. Broad classes can be used emphasizing dominant species, or on the other hand rare species can be emphasized by dividing low coverage values into several levels. Samples can be omitted, group size for divisions and the number of indicator species for divisions

can be chosen, as well as the number of species in the final tabulation and the weight of species in the analysis. Species can also be omitted from the list of potential indicators. In this analysis, the default values were used. -TWINSpan was recently used in classifying and ordinating forest ecosystems in the Great Claybelt of northeastern Ontario, and the authors expressed satisfaction with the potential of TWINSpan (Jones *et al.* 1982).

TWINSpan-runs were performed for all the sites together, as well as for Areas I and II separately. Area III was not analyzed separately, due to the small number of sample sites and the occurrence of mineral soil sites in the sampling.

The environmental data for water and peat were analyzed using the statistical package SPSSX (Anon. 1983). The means and standard deviations of the water and peat parameters were calculated for each vegetation group, and a series of one-way analyses of variance and comparisons of means was performed between the groups to determine whether the groups differed significantly in respect to any of the measured environmental factors. This was done to assess the capability of the vegetation groups to reflect environmental variation. Means were compared by Scheffé's method, which, according to Steel and Torrie (1980), is appropriate for looking at contrasts suggested by the data and is suited for unequal replications, which was the case in this analysis.

A problem arose considering water and peat pH-values and their statistical treatment. These parameters are logarithmic by nature and should not be averaged arithmetically. The correct way of determining mean pH-values is to convert the pH-data into H^+ -concentrations, carry out the calculations with these values and convert the results back into pH-values. However, even with little variation in the pH-values, this method conveys a distorted picture, because a few low pH-values make the mean H^+ -ion concentration rise greatly and respectively drop the overall mean pH, which then is not representative of the pH-conditions as they really are in the field. The arithmetical averaging was therefore accepted for the vegetation groups in this study, but for the overall description of the study areas, median values and ranges are given.

In addition to TWINSpan, ordinations using DECORANA (Hill 1979a), a detrended correspondence analysis (DCA) technique from the Cornell Ecological Package, were carried out. DECORANA was run on both data sets for all plots and separately for Areas I and II.

DECORANA uses the species-by-samples-matrix as a primary datum. From this primary data matrix, a secondary matrix is computed, having a dissimilarity or distance value for every pair of samples. This results in a samples-by-samples-dissimilarity matrix. Geometrically, this can be conceived as follows: axis 1 is the dissimilarity to

sample 1 , axis 2 the dissimilarity to sample 2, and so on. Axes are ranked by their eigenvalues, which indicate how much of the variance is accounted for by each axis. Usually the two first axes convey enough information from the directions of ecological variation in the data. DECORANA is derived from reciprocal averaging, correcting for the faults found in RA (Gauch 1982). The relationship between the first and the second axes, which causes the so-called 'arch effect', is eliminated by detrending. Axis 1 is divided into segments and in these segments axis 2 scores are adjusted to an average of zero. Also, DCA results in a uniform axis scaling, achieving a uniform rate of species turnover along the ordination axis so that equal distances in the ordination correspond to equal differences in species composition.

To compare the results of the TWINSpan- and DECORANA-analyses, the sample ordination scores of the first two axes of DECORANA-ordinations were plotted using a FORTRAN-program (Boyd 1984), and the corresponding TWINSpan-groups were superimposed on this scattergram.

III. Results and discussion

A. Characterization of the study areas

pH of mire waters is used as a general discriminant of peatland types. Values presented by Sjörs (1952), and widely applied in North America, are:

- bogs ('mosses') 3.7-4.2
- extremely poor fens 3.8-5.0
- transitional poor fens 4.8-5.7
- intermediate fens 5.2-6.4
- transitional rich fens 5.8-7.0
- extreme rich fens 7.0-8.4

The majority of the sites in this study were in the transitional rich fen category, though differences could be found between areas (Table 2). Area I with a median value of 6.7 (range 4.10-7.22) represented transitional rich fens, while Area II (median value of 6.98 with a range of 6.57-7.53) was close to extreme rich fen type. Rich fen indicator species, as Scorpidium scorpioides or Drepanocladus revolvens (Slack *et. al.*), were not found, however.

The electric conductivity values of mire waters for the study areas were high. The overall average conductivity (117 μ S) was somewhat lower than in three rich fens areas in western Alberta, near Rocky Mountain House, Hinton and Edson, (Slack *et. al.* 1980), where conductivity varied between 140-456 μ S. The areal averages of calcium in water

Table 2. Means and standard deviations of important water and peat properties (the median value and range for water and peat pH) and tree cover on the three study areas. ^{1 2}

Area	I	II	III
# of sample sites	71	39	21
water properties:			
pH	6.7 (4.1-7.2) (38)	7.0 (6.6-7.5) (13)	6.2 (4.0-7.0) (7)
cond., μ S	111 $\pm$ 38.4 (36)	200 $\pm$ 38.9 (13)	90 $\pm$ 83.1 (7)
Ca, ppm	20 $\pm$ 7.7 (42)	57 $\pm$ 11.4 (13)	28 $\pm$ 29.3 (7)
peat properties:			
pH	6.3 (3.4-6.7) (37)	7.0 (6.4-7.5) (15)	5.8 (3.8-7.1) (7)
total N, %	1.65 $\pm$ 0.5 (37)	1.31 $\pm$ 0.5 (15)	1.26 $\pm$ 0.3 (7)
C/N-ratio	30 $\pm$ 12 (37)	32 $\pm$ 10 (15)	39 $\pm$ 13 (7)
total P, %	0.117 $\pm$ 0.04 (37)	0.086 $\pm$ 0.03 (15)	0.090 $\pm$ 0.02 (7)
Ca, %	1.62 $\pm$ 0.4 (37)	2.34 $\pm$ 0.6 (15)	1.52 $\pm$ 0.9 (7)
ash, %	12.9 $\pm$ 5.6 (37)	18.1 $\pm$ 7.5 (14)	12.0 $\pm$ 4.3 (7)
depth, cm	121 $\pm$ 38 (30)	56 $\pm$ 22 (14)	89 $\pm$ 45 (7)
tree species, basal areas, m ² /ha:			
bl. spruce	7.6 $\pm$ 7.8 (71)	11.3 $\pm$ 6.5 (39)	not
tamarack	5.8 $\pm$ 6.1 (71)	-	calculated

¹Complete list of all sampled properties in Appendix 1

²Sample size for each mean shown in brackets

in this study (20, 57 and 28 ppm) were comparable to the values of the western fens, where calcium varied between 18-37 ppm; the values of Area II even exceeded the rich fen values. The water pH-values of this study did not reach those of the rich fens, which ranged between 6.8 and 7.9. Another comparison to Albertan peatlands can be made to poor fens in the Swan Hills (Vitt *et al.* 1975), where the range in water pH was 4.1-6.0 with a mean value of 5.2 (n=48), and the average calcium concentration 2.3 ppm. The peatlands in this study were thus close to rich fens in their water chemistry.

Of the specific ions, Ca^{2+} - and Mg^{2+} -concentrations were highest on Area II. Na^{+} - and K^{+} - values were recorded only on Area I. Na^{+} and K^{+} are not indicative of the nutrient status of peatlands, but can give information on other things. Sodium is used to describe maritime-continentality influences on peatlands (e.g. Sims *et al.* 1982), and is higher on areas influenced by sea winds carrying salty sprays. Potassium correlates fairly well with the water conditions on a site: wet sites have lower potassium contents than dry sites, because this element is water soluble and leaches out easily (Heikurainen 1979).

The two main study areas differed considerably in their physiognomy. Area I was wet, with frequent large pools of open water. The average water table depth was 18 (± 17 , n=28) cm. Mean peat depth exceeded 120 cm, and depths over 300 cm were recorded in the eastern part of the area (Gillard

1984)³. The levels of major peat nutrients, nitrogen and phosphorus, were highest on area I (1.65 ± 0.5 %, $n=37$ and 0.117 ± 0.04 %, $n=37$, respectively), whereas peat C/N-ratios were similar on both areas. Area II was drier and hummocky, and the water table was deeper than on Area I, averaging 34 (± 6 , $n=3$) cm. The peat layer was shallow and averaged less than 60 cm. Water pH and electric conductivity values were highest on Area II (median value of 6.98, and mean of 200 ± 38.9 μ S, $n=13$, respectively). Peat was eutrophic, with a median pH of 7.05 (range 6.39-7.52, $n=15$), mean ash content of 18.1 (± 7.5 , $n=14$) % and mean calcium content of 2.3 (± 0.6 , $n=15$) %.

The forest cover was variable on Area I. Tamarack occurred, either in mixed stands with black spruce or alone, on fifty-three sites and dominated thirty-two of them (Photographs 1 and 2). Black spruce prevailed on Area II, with tamarack occurring only on five sites. Lesser vegetation was also more homogenous on Area II.

B. TWINSPAN-analyses, all sites

NOTREES data set

In the analysis of all sites with the NOTREES data set, eight vegetation groups were defined, each characterized by a set of indicator species (Figure 2).

³Personal communication: Discussion, Dec. 1984



1



2

Photographs 1 and 2. Lichen-covered black spruce - tamarack
- forest on study area I in late spring (1) and in July (2).

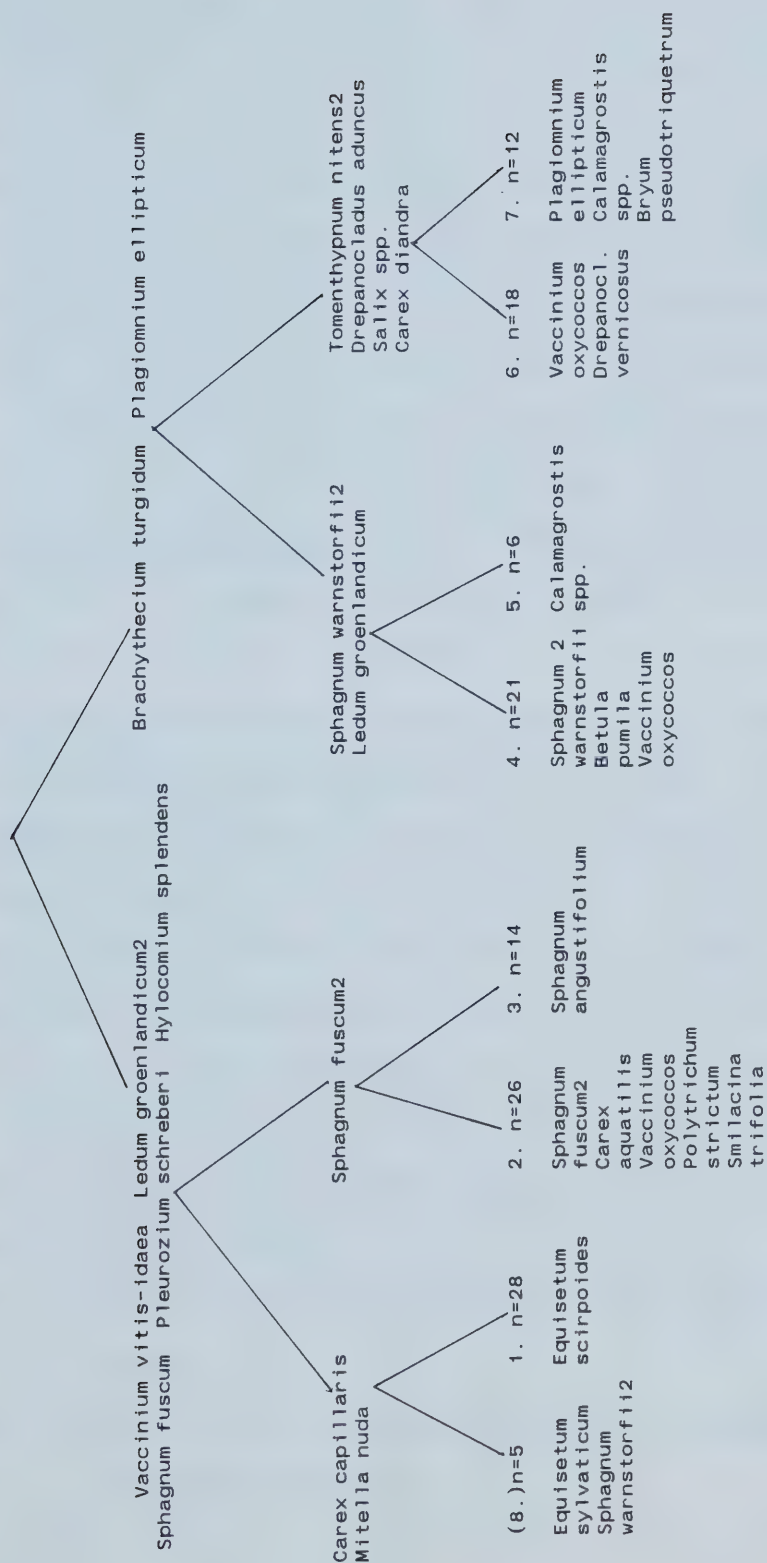


Figure 2. TWINSpan-analysis for all sites with the NOTREES data set; the indicator species and the number of sample sites of vegetation groups 1-8. Pseudospecies cut level indicated after species name if other than the first.

The number of sample sites in the groups varied between 6 and 28. A definite outlier, group 8 (extreme left) was excluded from further analysis, because it consisted of mineral soil sites occupied by white spruce from Area III. The analysis was stopped at the fourth level, as the next level produced too many small groups and decreased sample size for statistical testing of water and peat parameters.

Vegetation groups 1 and 2 represented mainly areas II and III, characterized by feathermosses (here used to refer to Hylocomium splendens (Hedw.) BSG and Pleurozium schreberi (Brid.) Mitt.), Ledum and Sphagnum fuscum (Photographs 3 and 4). Sites from Area I were mainly in vegetation groups 4-7, which were described by several brown mosses (here used to refer to Brachythecium turgidum (C.J. Hartm.) Kindb., Plagiomnium ellipticum (Brid.) Kop., Drepanocladus spp., Calliergon giganteum (Schimp.) Kindb.) and Bryum pseudotriquetrum (Hedw.) Gaertner *et al.*). Thus the defined vegetation groups coincided mainly with the three study areas, reflecting differences in their vegetation.

The outcome of the analysis can be summarized as follows, giving each vegetation group an indicator species from all three levels:

- group 1: feathermoss - Mitella nuda - Equisetum scirpoides-
group
- group 2: feathermoss - Sphagnum fuscum - Polytrichum
strictum -group



Photograph 3. Black spruce-Ledum-Pleurozium-site on Area III, representing vegetation group 3 in Figures 2 and 3.



Photograph 4. Pleurozium schreberi covering forest floor on a dry site.

group 3: feathermoss - Sphagnum fuscum - Sphagnum angustifolium-group

group 4: brown moss - Sphagnum warnstorffii - Betula pumila -group

group 5: brown moss - Sphagnum warnstorffii - Calamagrostis -group

group 6: brown moss - Tomenthypnum - V. oxycoccos -group

group 7: brown moss - Tomenthypnum - Calamagrostis -group

Most indicator species on the feathermoss-side indicated ombrotrophic to oligo-mesotrophic conditions. Ombrotrophy on these areas occurred mostly in dry microhabitats, as hummocks, which were isolated from the minerotrophic waters. It was best manifested by Sph. fuscum. The occurrence of Sph. angustifolium (Russ.) C.Jens. was suggestive of weakly minerotrophic conditions. On the other hand, most of the indicators of the brown moss-groups suggested meso-eutrophic site conditions. These were Brachythecium and Plagiomnium, which grew in small patches in wet microhabitats, and Sph. warnstorffii and Tomenthypnum, which covered larger surfaces on low moist hummocks. The ombro- or oligotrophic indicators like Ledum and Vaccinium oxycoccos L. occurred also on these sites in the dry microhabitats.

Tabulation of water and peat properties for the vegetation groups revealed a high degree of similarity. Differences and variability between mean values were small (Table 3a). For example, water pH-values varied from 5.75 to

Table 3a. Means and standard deviations of important water and peat properties and tree cover of the TWINSpan-vegetation groups; all sites, NOTREES data set¹

vegetation group	(8)	1	2	3	4	5	6	7
# of plots	6	28	26	14	21	6	18	12
location								
area I		14 %	15 %	86 %	100 %	100 %	83 %	75 %
area II		71 %	46 %				17 %	25 %
area III	100 %	14 %	38 %	14 %				
water properties:								
pH	6.59 ± .34	7.02 ± .32	6.18 ± 1.38	5.75 ± .97	6.74 ± .23	6.11 ± .57	6.82 ± .18	6.79 ± .21
cond. μ S	74 ± 35.1	204 ± 56.5	139 ± 81.9	71 ± 29.8	120 ± 31.6	108 ± 6.4	114 ± 30.9	152 ± 53.0
Ca, ppm	24 ± 8.5	59 ± 20.5	38 ± 24.3	16 ± 6.2	21 ± 5.3	19 ± 11.8	18 ± 5.1	32 ± 19.1
peat properties:								
pH	6.18 ± .31	6.82 ± .52	5.92 ± 1.66	5.80 ± .90	6.29 ± .24	6.31 ± .17	6.25 ± .17	6.45 ± .34
C, %	43 ± 1.8	40 ± 8.0	43 ± 3.4	44 ± 6.0	45 ± 1.9	46 ± 2.0	46 ± 1.0	44 ± 4.1
N, %	1.50 ± .11	1.27 ± .33	1.04 ± .42	1.24 ± .31	1.55 ± .29	1.58 ± .52	2.05 ± .27	2.03 ± .23
C/N	29 ± 3.2	32 ± 5.1	48 ± 21.0	36 ± 6.8	30 ± 5.4	31 ± 8.9	23 ± 3.0	22 ± 3.2
P, %	.111 ± .004	.085 ± .022	.070 ± .018	.084 ± .023	.141 ± .044	.090 ± .028	.118 ± .016	.134 ± .037
Ca, %	2.0 ± .2	1.2 ± .7	1.6 ± .7	1.7 ± .8	2.3 ± .5	0.9 ± .5	1.8 ± .9	1.3 ± .6
depth, cm	107 ± 51	51 ± 26	93 ± 33	97 ± 52	126 ± 31	95 ± 7.1	150 ± .	109 ± 47
tree species, ba m ² /ha:								
bl.spruce	4.5 ± 3.5	16.5 ± 3.2	7.0 ± 2.0	15.5 ± 7.7	5.5 ± 1.8	11.4 ± 2.2	1.2 ± 0.9	2.1 ± 1.3
tamarack	1.9 ± 3.0	0.4 ± 1.1	0.5 ± 0.8	2.3 ± 2.0	9.0 ± 3.0	6.7 ± 5.2	5.0 ± 3.2	6.1 ± 3.7
wh.spruce	3.6 ± 4.0							

¹Complete list in Appendix 2.

7.02 with an overall average of 6.4. Peat pH varied even less, from 5.80 to 6.80 with an average of 6.3. Although no clear trends were discernible, a reflection of the vegetational division into ombrotrophic or oligotrophic versus meso-eutrophic sites was demonstrable in some important environmental parameters. The values of peat and water pH, as well as peat nitrogen and phosphorus, were lowest in feathermoss - Sph. fuscum - groups 1-3 and highest in brown moss-characterized groups 4-7. The reverse was true for peat C/N-ratio, which was highest in the Sph. fuscum-group. In contrast with these trends were the high minerotrophy values (conductivity, Ca^{2+} , Mg^{2+} -concentrations) in group 1; these can probably be attributed to the shallow peat layer of these sites.

Black spruce stands with high basal areas were found in the feathermoss - groups, completing the picture of a typical 'muskeg' plant community. Black spruce appeared also in the brown moss-groups, where the highest basal areas of tamarack were found. Tamarack stands were generally sparser than black spruce stands.

From the twenty-three environmental properties measured, only nine showed significant differences among the vegetation groups (Table 3b). The statistical analysis with these TWINSpan-groups, as with all the groups that follow, was indicative of general trends in the data only, due to the small sample sizes. The differences were consistently between groups 1, 2 and 3 versus 4, 5, 6 and 7, which were

at opposite ends of the trophic gradient as demonstrated by the indicator species. On the other hand, due to their composition, groups representing Areas II and III were generally contrasted with those representing Area I. Peat nitrogen and phosphorus were the most important parameters showing differences between the groups. Peat nitrogen content in groups 6 and 7 exceeded 2 %, whereas groups 1-3 had less than 1.3 % nitrogen. The highest values of peat phosphorus were in groups 4 and 7 (0.13 and 0.14 %) and the lowest in groups 1-3 (about 0.08 %). The soluble forms of these nutrients (ammonium, nitrate, phosphate) did not differ significantly among any groups.

Table 3b. The significant differences among the vegetation groups of the TWINSpan-analysis for all plots, NOTREES data set.

(Low value group : high value group)

Water chemistry

conductivity	3:1
Ca , Mg	3:1 ; 6:1 ; 5:1 ; 4:1
Na	1:4 ; 2:4

Peat chemistry

N	2:7 ; 3:7 ; 1:7 ; 2:6 ; 3:6 ; 1:6
P	2:7 ; 1:7 ; 2:4 ; 3:4 ; 1:4
C/N-ratio	7:2 ; 6:2 ; 4:2

Peat depth	1:4 ; 1:6
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Black spruce basal area	6:5 ; 6:3 ; 7:3 ; 4:3 ; 2:3 ; 6:1 ; 7:1 ; 4:1 ; 2:1
-------------------------	--

BASAL data set

The outcome of the TWINSpan-analysis with the BASAL data set produced eight groups, with 5-28 sites in each (Figure 3). Again, seven groups were used in further analysis. The composition of groups and their division between the areas were very similar to the NOTREES-analysis, with the addition of the tree species as prominent indicators. Black spruce appeared in the main division together with the feathermoss-side species from the NOTREES-analysis. On the other side, tamarack displaced the two brown mosses as main indicators. With tamarack occurring mainly on Area I, sites from that area occupied the tamarack-side, and sites from Areas II and III were chiefly on the black spruce-side.

The outcome of the analysis can be summarized in the following groups:

group 1: black spruce - Rubus - Linnaea - Tomenthypnum
-group

group 2: black spruce - Sphagnum fuscum - Polytrichum
strictum -group

group 3: black spruce - Sphagnum fuscum - feathermoss -group

group 4: tamarack - black spruce - Betula pumila -group

group 5: tamarack - black spruce - Calamagrostis -group

group 6: tamarack - Carex diandra - Betula pumila -group

group 7: tamarack - Carex diandra - brown moss -group

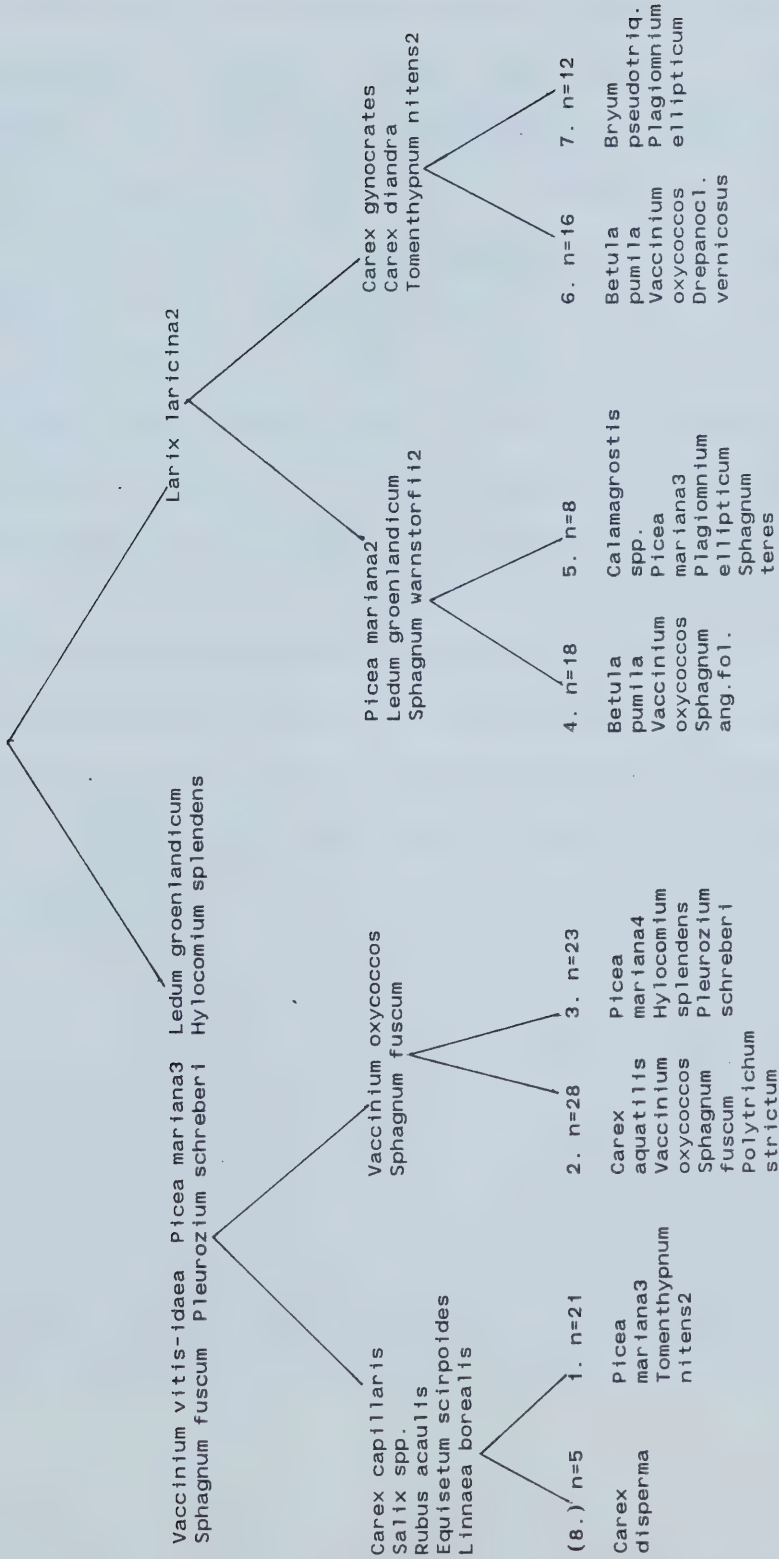


Figure 3. TWINSpan-analysis for all sites with the BASAL data set; the indicator species and the number of sample sites of vegetation groups 1-8. Pseudospecies cut level indicated after species name if other than the first.

The tree species on opposite sides in the main dichotomy made the division clearer. Most indicators associated with black spruce, especially in vegetation groups 2 and 3, were typical of dry microhabitats (Ledum, feathermosses) and poor nutrient status (Sph. fuscum). The indicators in group 1 (Carex capillaris L., Tomenthypnum nitens) characterized the most highly ionic sites on Area II. With tamarack, species of typically wetter and more strongly ionic conditions occurred (Betula pumila L., brown mosses), in association with hummock-growing species (e.g. Carex gynocrates Wormsk, Vacc. oxycoccos) (Photographs 5-7).

Comparison and analysis of water and peat properties in the vegetation groups was mostly the same as in the NOTREES-analysis (Tables 4a, 4b). There were some more differences in the peat chemistry but they showed the same trends between the black spruce-feathermoss-sites versus tamarack-sites.



Photographs 5 and 6. Tamarack - sites on Area I with abundant understory vegetation (vegetation group 5 in Figures 4 and 5).

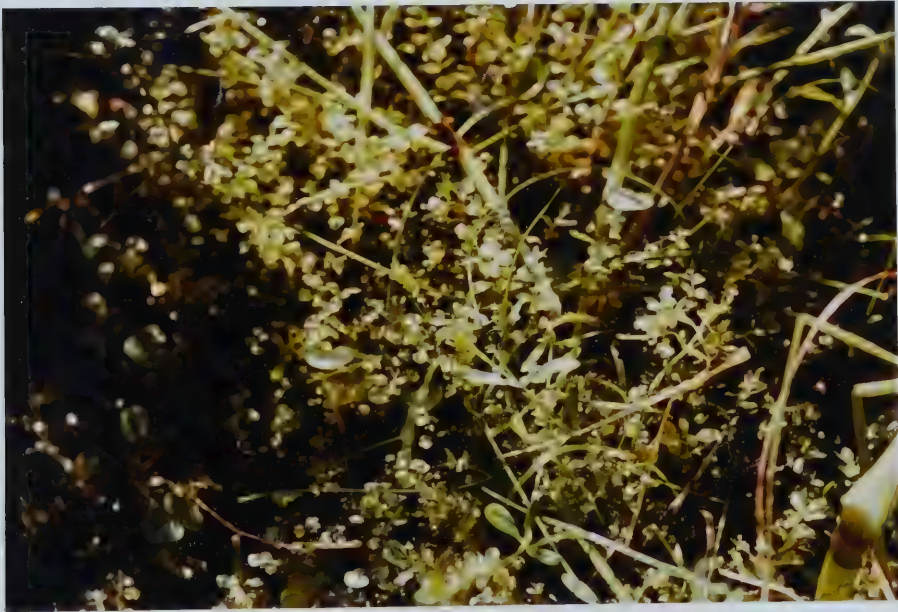
Table 4a. Means and standard deviations of important water and peat properties and tree cover of the TWINSPAN-vegetation groups; all sites, BASAL data set¹

vegetation group	(8)	1	2	3	4	5	6	7
# of sites	5	21	28	23	18	8	16	12
location								
area I		5 %	14 %	74 %	100 %	100 %	87 %	85 %
area II		81 %	50 %	13 %			13 %	15 %
area III	100 %	14 %	36 %	13 %				
water properties:								
pH	6.55 ± .47	7.02 ± .32	6.25 ± 1.33	5.89 ± .93	6.85 ± .21	6.14 ± .52	6.80 ± .11	6.79 ± .21
cond., μ s	75 ± 49.5	204 ± 56.5	128 ± 77.5	79 ± 32.3	123 ± 34.3	119 ± 8.9	109 ± 35.8	152 ± 53.0
Ca, ppm	25 ± 12.0	59 ± 20.5	35 ± 24.3	18 ± 7.3	20 ± 5.5	20 ± 10.4	19 ± 5.4	32 ± 19.1
peat properties:								
pH	6.11 ± .40	6.88 ± .49	6.00 ± 1.49	5.89 ± .80	6.26 ± .25	6.30 ± .19	6.28 ± .20	6.45 ± .34
N, %	1.50 ± .16	1.27 ± .35	1.12 ± .42	1.25 ± .28	1.64 ± .32	1.60 ± .39	2.06 ± .30	2.03 ± .23
P, %	.113 ± .001	.083 ± .022	.075 ± .020	.090 ± .031	.142 ± .048	.100 ± .019	.125 ± .018	.134 ± .037
Ca, %	2.0 ± .23	2.5 ± .5	1.6 ± 1.0	1.6 ± .6	1.5 ± .24	1.7 ± .31	1.6 ± .18	1.8 ± .32
depth, cm	135 ± 21	51 ± 26	94 ± 38	98 ± 48	123 ± 34	113 ± 32	150 ± -	109 ± 47
tree species, basal area m ² /ha:								
bl. spruce	1.7 ± 1.6	16.2 ± 3.7	5.8 ± 2.0	16.7 ± 7.0	5.2 ± 5.3	11.2 ± 5.6	0.5 ± 0.5	2.2 ± 1.3
tamarack	1.7 ± 0.4	0.5 ± 1.3	0.3 ± 0.5	1.6 ± 1.9	10.1 ± 2.5	7.6 ± 3.1	4.7 ± 3.2	6.1 ± 3.7
wh. spruce	9.8 ± 5.5							

¹Complete list in Appendix 3.

Table 4b. The significant differences among the vegetation groups of the TWINSpan-analysis for all plots, BASAL data set.

(Low value group : high value group)	
Water chemistry	
pH	3:1
Ca , Mg	3:1 ; 6:1 ; 4:1 ; 5:1
Peat chemistry	
N	2:7 ; 2:6 ; 3:7 ; 3:6 ; 1:7 ; 1:6
P	2:7 ; 2:4 ; 1:4
Ca	4:1
C/N-ratio	7:2 ; 6:2
Peat depth	1:4 ; 1:6
Black spruce basal area	
	6:5 ; 6:3 ; 6:1 ; 7:3 ; 7:1 ; 4:3 ; 4:1 ; 2:3 ; 2:1
Tamarack basal area	
	2:4



Photograph 7. Plagiomnium ellipticum, an important indicator species in the TWINSpan-analyses.

C. TWINSPAN-analyses, Area I

NOTREES data set

To eliminate the variation due to differences among areas, the two main study areas were analyzed separately. This stratification of the data resulted in clearer relationships between vegetation and measured environmental parameters. Area I was the more interesting of the two because of the greater variability in its vegetation.

The TWINSPAN-analysis with the NOTREES-data set (Figure 4) revealed a definite vegetative gradient in the data, placing sites with indicators of poor nutrient status apart from sites with indicators of richer conditions. Eight groups were produced, 5-14 sites in each.

The indicators in the main division were the same as in the analysis of all sites. Most of the sites (fifty-one) were in the five groups featured by brown mosses Brachythecium and Plagiomnium. There were only three groups (twenty-one sites) featured by feathermosses, showing that ombro- or oligotrophic conditions were rare on Area I.

The groups can be summarized as follows:

group 1: feathermoss - Ledum - Sphagnum fuscum -group

group 2: feathermoss - Ledum - Sphagnum angustifolium -

Salix-group

group 3: feathermoss - Ledum - Sphagnum warnstorffii -group

group 4: brown moss - Calamagrostis - Sphagnum teres -group

group 5: brown moss - Calamagrostis - Betula pumila -group

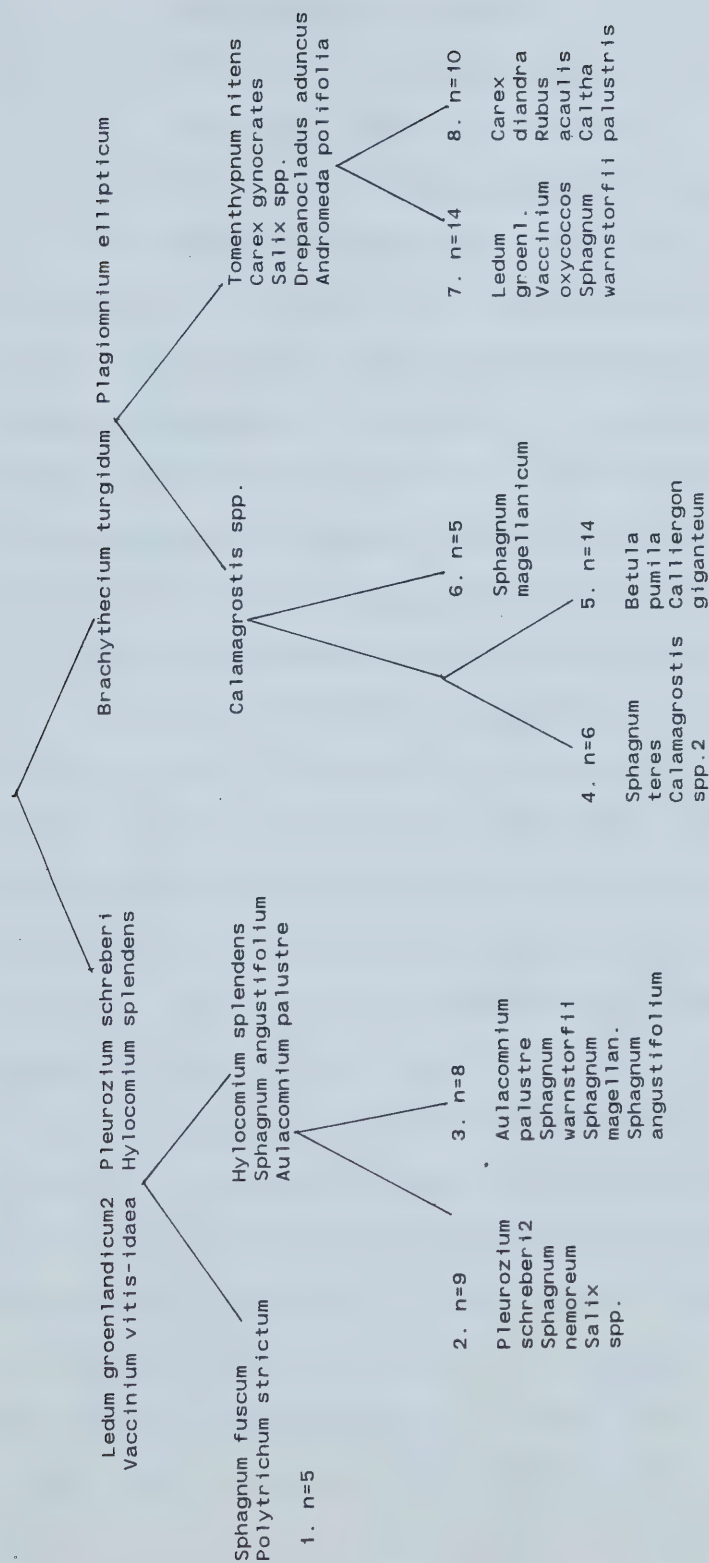


Figure 4. TWINSpan-analysis for Area I with the NOTREES data set; the indicator species and the number of sample sites of vegetation groups 1-8. Pseudospecies cut level indicated after the species name if other than the first.

group 6: brown moss - Calamagrostis - Sphagnum
magellanicum -group

group 7: brown moss - Tomenthypnum
Sphagnum warnstorffii-group

group 8: brown moss - Tomenthypnum - Caltha palustris -group

The Sphagnum-mosses in groups 1 to 3 denoted a gradient from ombro- or oligotrophic (Sph. fuscum) through ombro- or oligo(-meso)trophic (Sph. angustifolium) to meso-eutrophic (Sph. warnstorffii) conditions. In groups 4-8, the indicator species were suggestive of wet and sparsely forested sites (Betula pumila, Caltha) and meso-eutrophic conditions (all bryophytes, except Sph. magellanicum Brid, which was typical of shady low hummocks in tamarack stands).

The water and peat properties of the vegetation groups were very similar also in this analysis (Table 5a). However, a discernible environmental gradient was displayed and supported by the statistical analysis (Table 5b), where the feathermoss-side was contrasted with the brown moss-side. A distinct peat nitrogen gradient was demonstrable: the Sph. fuscum-group (group 1) had the lowest value (0.78 %), the brown moss-Caltha -group (group 8) the highest (2.24%). Peat phosphorus showed the same trend, being low in the feathermoss-groups (average 0.075%) and higher in the brown moss-groups (average 0.127%). Group 1 was distinctly different from the others in its carbon/nitrogen-ratio, but the standard deviation was large as well (67±36.3). The trend was evident for the feathermoss-groups to have a

Table 5a. Means and standard deviations of important water and peat properties and tree cover of the TWINSpan-vegetation groups: Area I, NOTREES data set¹

vegetation group	1	2	3	4	5	6	7	8
# of sites	5	9	8	6	14	5	14	10
water properties:								
pH	5.06 ± 1.35	6.25 ± .69	5.72 ± .95	6.30 ± .69	6.79 ± .10	6.66 ± .76	6.68 ± .05	6.82 ± .12
cond., μ S	55 ± 20.5	80 ± 21.7	73 ± 38.2	116 ± 10.2	124 ± 33.4	153 ± 38.9	118 ± 14.8	123 ± 51.9
Ca, ppm	12 ± 11.3	21 ± 6.4	13 ± 5.7	20 ± 10.2	22 ± 6.2	21 ± 8.1	18 ± 4.2	21 ± 10.1
peat properties:								
pH	4.85 ± 1.99	6.23 ± .42	5.96 ± .72	6.30 ± .16	6.28 ± .33	6.27 ± .02	6.28 ± .11	6.38 ± .27
N, %	0.78 ± .37	1.25 ± .31	1.43 ± .08	1.50 ± .41	1.75 ± .32	1.47 ± .25	1.88 ± .23	2.24 ± .17
C/N	67 ± 36.3	36 ± 5.2	32 ± 2.7	32 ± 7.0	26 ± 5.6	31 ± 3.8	25 ± 3.4	21 ± 1.8
P, %	.054 ± .009	.088 ± .026	.082 ± .005	.090 ± .015	.163 ± .043	.141 ± .021	.117 ± .019	.124 ± .014
Ca, %	1.2 ± 1.5	1.8 ± .4	1.6 ± .5	1.8 ± .3	1.7 ± .4	1.5 ± .3	1.5 ± .3	1.6 ± .2
depth, cm	90 ± 84.9	95 ± 37.0	130 ± 34.6	125 ± 28.9	121 ± 34.4	150 ± -	150 ± -	130 ± 34.6
tree species, basal area m ² /ha:								
bl.spruce	11.9 ± 5.2	15.5 ± 9.0	17.2 ± 7.2	8.2 ± 4.2	4.7 ± 2.0	7.7 ± 4.9	2.1 ± 0.9	1.5 ± 1.6
tamarack	1.8 ± 1.0	1.4 ± 1.6	5.0 ± 3.1	5.9 ± 4.6	8.8 ± 2.5	9.5 ± 5.3	7.3 ± 4.0	6.1 ± 2.2

¹Complete list in Appendix 4.

higher C/N-ratio than the brown moss-groups. Group 1 had also the lowest groundwater pH and conductivity values (5.06 ± 1.35 and $55 \pm 20.5 \mu\text{S}$, respectively).

Black spruce prevailed on the feathermoss-side, which was also most heavily forested. There was a detectable gradient from denser stands to more open forests from group 1 to group 8: tamarack stands were throughout more sparsely forested. On this area they were also associated with the deepest peat layers.

Table 5b. The significant differences among the vegetation groups of the TWINSpan-analysis for Area I, NOTREES data set.

(Low value group : high value group)

Water chemistry

pH	1:5 ; 1:8
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Peat chemistry

N	1:5 ; 1:7 ; 1:8 ; 2:8
P	1:5 ; 3:5 ; 4:5 ; 2:5
C/N-ratio	all:1

Black spruce basal area	7:2 ; 7:3 ; 8:3 ; 5:2 ; 5:3
-------------------------	-----------------------------

BASAL data set

The result of the TWINSpan-analysis using the BASAL-data set for Area I was very similar to the NOTREES-analysis (Figure 5). Seven groups were distinguished, with 5-14 sites in each. Indicator species were mostly the same, with the addition of black spruce to the main division and to a lower level on the brown moss-side. As in the NOTREES-analysis, the result showed an environmental gradient in the indicator species, from poor nutrient status indicators (Ledum, Aulacomnium, Sph. fuscum and Sph. nemoreum) to indicators of a richer status (Plagiomnium, Drepanocladus, Sph. warnstorffii (Photograph 8), Tomenthypnum, Bryum).

The groups can be summarized as follows:

- group 1: black spruce - Ledum - Sphagnum fuscum -group
- group 2: black spruce - Ledum - Aulacomnium palustre -group
- group 3: Betula pumila - black spruce - Drepanocladus vernicosus - Calamagrostis -group
- group 4: Betula pumila - black spruce - Vaccinium oxycoccos -group
- group 5: Betula pumila - black spruce - Sphagnum warnstorffii -group
- group 6: Betula pumila - Salix - Tomenthypnum - Ledum - Vaccinium oxycoccos -group
- group 7: Betula pumila - Salix - Tomenthypnum - Bryum - group

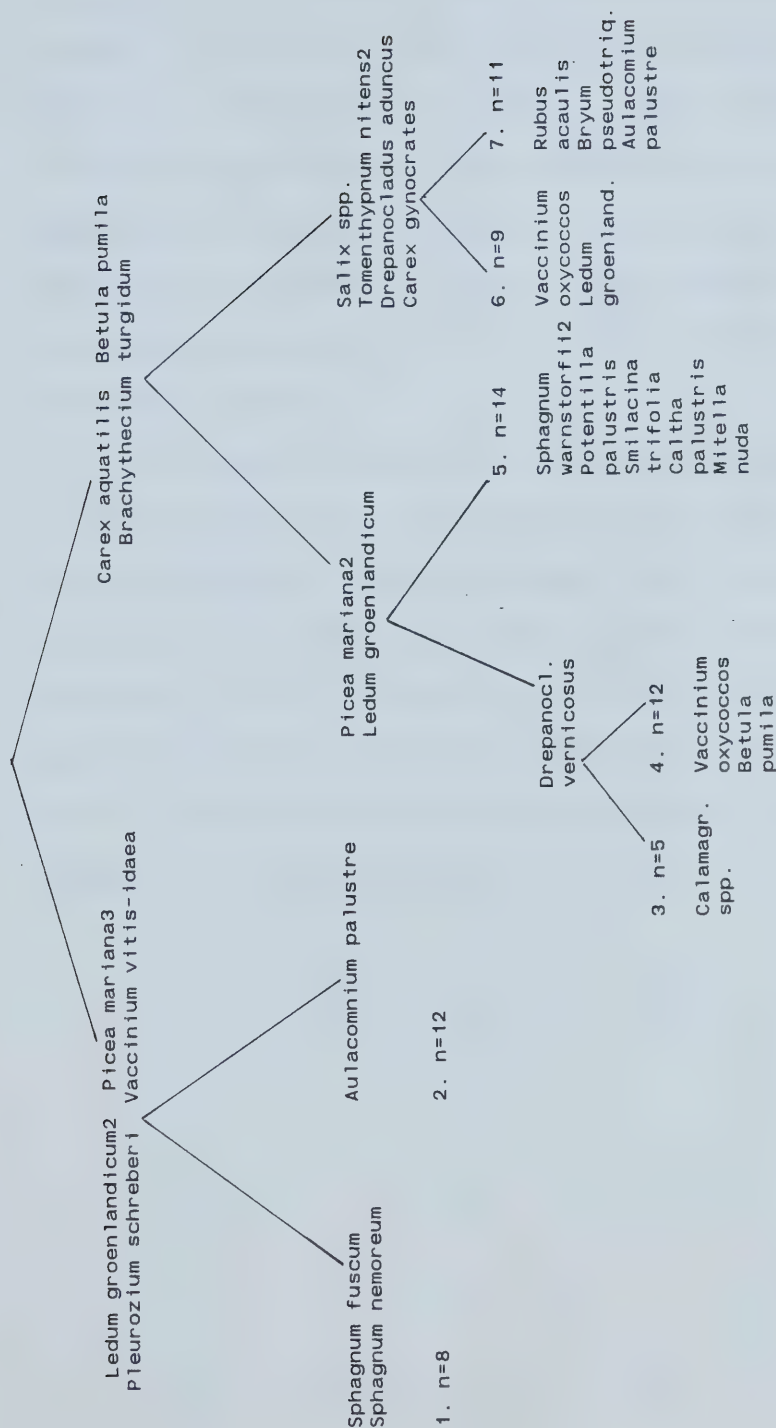


Figure 5. TWINSpan-analysis for Area I with the BASAL data set; the indicator species and the number of sample sites of the vegetation groups 1-7.

Pseudospecies cut level indicated after species name if other than the first.

Black spruce appeared as an indicator, but tamarack did not for any of the levels studied. Moreover, black spruce was associated with the same plant species identified earlier in the analysis of all sites. Thus black spruce showed more fidelity to a certain plant community, whereas in the tamarack stands there was much more variation in the understory. This was mainly due to the variable water level conditions on tamarack sites, which resulted in numerous microhabitats (pools, lawns, carpets, hummocks) for different species.

Environmental gradients were demonstrable also in this analysis (Table 6a). As in the NOTREES-analysis, the feathermoss-black spruce groups 1 and 2 were generally contrasted with the brown moss groups (Table 6b). In peat nitrogen content, there were additional differences between the highest value, group 7, and groups 4 and 5. The high black spruce basal area values of groups 1 and 2 were notably different from those of almost all other groups.

Table 6a. Means and standard deviations of important water and peat properties and tree cover of the TWINSpan-vegetation groups; Area I, BASAL data set¹

vegetation group	1	2	3	4	5	6	7
# of sites	5	12	14	9	11	8	12
water properties:							
pH	5.59 ± 1.07	6.14 ± .77	5.95 ± .52	6.69 ± .28	6.90 ± .19	6.67 ± .06	6.82 ± .11
cond, μ S	65 ± 26.8	82 ± 30.1	112 ± -	106 ± 15.0	128 ± 30.2	126 ± 12.2	129 ± 51.3
Ca, ppm	16 ± 8.1	18 ± 8.0	19 ± 13.6	17 ± 2.0	22 ± 4.9	20 ± 4.6	23 ± 10.0
peat properties:							
pH	5.42 ± 1.38	6.15 ± .53	6.33 ± .24	6.25 ± .11	6.33 ± .27	6.26 ± .27	6.35 ± .33
N, %	0.95 ± .44	1.33 ± .14	1.82 ± .45	1.58 ± .20	1.60 ± .34	1.97 ± .16	2.20 ± .18
C/N	51 ± 27.9	35 ± 3.9	27 ± 5.8	30 ± 3.6	29 ± 6.3	23 ± 2.6	21 ± 1.8
P, %	.070 ± .035	.082 ± .009	.100 ± .032	.132 ± .051	.152 ± .044	.112 ± .004	.127 ± .015
Ca, %	1.4 ± 1.0	1.8 ± .4	1.8 ± .4	1.5 ± .1	1.6 ± .2	1.6 ± .3	1.7 ± .3
depth, cm	83 ± 49.9	114 ± 33.6	90 ± -	150 ± -	83 ± 50	114 ± 34	90 ± 25
tree species, basal area m ² /ha:							
bl. spruce	14.1 ± 6.4	18.7 ± 5.8	11.4 ± 2.4	4.2 ± 1.3	4.7 ± 1.4	0.9 ± .5	1.6 ± 1.5
tamarack	1.5 ± 1.3	2.9 ± 3.1	8.0 ± 4.5	7.0 ± 2.2	8.7 ± 2.5	6.7 ± 5.1	7.1 ± 2.4
water table depth, cm	40 ± 5	15 ± 6	20 ± 6	29 ± 35	9 ± 3	12 ± 5	17 ± 12
saturated hydraulic conductivity, cm/s × 10 ⁻⁴	8.7 ± 4.1	5.6 ± 2.4	14.9 ± 13.1	14.9 ± 15.2	11.0 ± 11.2	9.3 ± 3.7	6.9 ± 1.3

¹Complete list in Appendix 5.

Table 6b. The significant differences among the vegetation groups of the TWINSpan-analysis for Area I, BASAL data set.

(Low value group : high value group)

Water chemistry

pH 1:7 ; 1:5

Peat chemistry

N 1:5 ; 1:6 ; 1:7 ; 2:7 ; 4:7 ; 5:7

P 2:5 ; 1:5

C/N-ratio 7:1

Black spruce basal area 6:3 ; 6:1 ; 6:2 ; 7:1 ; 7:2 ;
4:1 ; 4:2 ; 5:1 ; 5:2



Photograph 8. Sphagnum warnstorffii, the most commonly occurring Sphagnum-species on Area I.

D. TWINSPAN-analysis, area II, both data sets

The results of the TWINSPAN-analysis for area II with both data sets are presented in Figure 6. In both analyses, three groups were distinguished, with 6-17 sites in each. The main division was between sites dominated by Sphagnum fuscum and those not dominated by it (Photographs 9 and 10). Some indicator species were different for the two data sets, but the composition of the groups stayed almost the same. The groups can be summarized as follows:

group 1: Sph. fuscum - Sph. angustifolium -

Betula pumila -group

group 2: Sph. fuscum - Carex capillaris -

Picea mariana -group

group 3: 'non-Fuscum' -group

Black spruce dominated Area II, with basal area values that were slightly below those of black spruce stands on Area I.

The water and peat properties were identical for the groups of both NOTREES and BASAL analyses (Tables 7a, 7b). Group 1 differed from the others with its low electric conductivity values. Peat nitrogen and phosphorus values on this area were similar to the lower values on Area I, with no significant differences among the vegetation groups. The base saturation values of peat differed significantly between groups 1 (64 ± 10.5) and 3 (86 ± 8.6). This property is used to measure the trophic status of peat, which was generally high on this area.



Photograph 9. Sphagnum fuscum- and (left) and Tomenthypnum nitens- hummocks on Area II.



Photograph 10. Three typical moss species from Area II: Sphagnum angustifolium (upper left corner), Sphagnum warnstorffii (middle) and Tomenthypnum nitens (to the right).

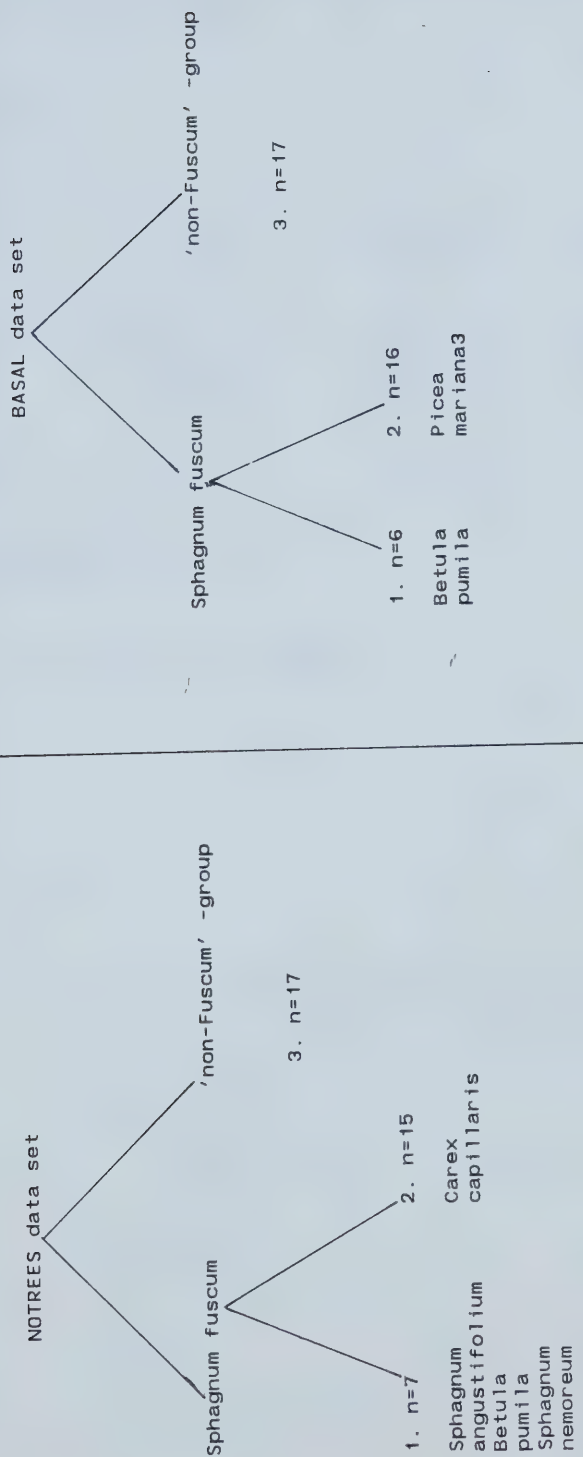


Figure 6. TWINSpan-analysis for Area II with both data sets; the indicator species and the number of sample sites of the vegetation groups 1-3. pseudospecies cut level indicated after species name if other than the first.

Table 7a. Means and standard deviations of important water and peat properties and tree cover of the TWINSPAN-vegetation groups;

Area II, both data sets¹

vegetation group	1	2	3
# of sites	6	16	17
water properties:			
pH	6.49 ± .25	7.07 ± .30	7.18 ± .29
cond,µS	64 ± 19.8	198 ± 28.0	214 ± 14.1
Ca,ppm	21 ± 5.4	55 ± 14.3	60 ± 2.8
peat properties:			
pH	6.04 ± .69	6.98 ± .94	6.95 ± .30
N,%	1.34 ± .88	1.24 ± .45	1.41 ± .51
C/N	32 ± 15.6	36 ± 10.8	28 ± 7.3
P,%	.075 ± .033	.080 ± .017	.093 ± .031
Ca,%	1.4 ± .2	2.3 ± .6	2.4 ±
Bas. satur.	64 ± 10.5	84 ± 9.2	86 ± 8.6
depth	80 ± -	84 ± 31.5	43 ± 18.3
tree species, basal area m ² /ha:			
bl.spruce	3.7 ± 6.7	10.9 ± 4.0	16.2 ± 2.1
tamarack	0.6 ± 0.2	---	0.5 ± 1.2

¹Complete list in Appendix 6.

Table 7b. The significant differences among the vegetation groups of the TWINSPAN-analysis for Area II, both data sets.

(Low value group : high value group)

Water chemistry

conductivity	1:2 ; 1:3
Ca, Mg	1:2 ; 1:3

Peat chemistry

Base saturation	1:3
Peat depth	3:2
Black spruce basal area	1:3 ; 2:3

E. Indicator species considerations

The indicator species in the TWINSPAN-results (Appendix 7) were common and frequently occurring peatland species. They are well documented in the literature (e.g. Sjörs 1950, Ruuhijärvi 1960, Slack *et al.* 1980 and the literature cited) and relatively easy to recognize with some experience and familiarity with peatland areas.

The indicator species indirectly conveyed information of the varying water conditions and the proportions of different microhabitats on each site, both variables for which data were not collected. A hummock-to-hollow gradient showed itself among the vegetation groups (e.g. Figure 4). Indicators in vegetation groups 1-3 were hummock-forming and -growing species: Sph. fuscum, feathermosses, Vaccinium vitis-idaea and V. oxycoccos, Ledum, Polytrichum strictum Brid., Equisetum scirpoides Michx. Moist microhabitats were occupied by Carex aquatilis Wahlenberg. and Sph. angustifolium, the former growing in shallow open water hollows, the latter on low hummocks above open water. On the other hand, most of the indicators of vegetation groups 4-8 were characteristic of moist, low hummocks, an intermediate position on the hummock-hollow gradient: Brachythecium turgidum, Sph. warnstorffii, Bryum pseudotriquetrum, Carex diandra Schrank, Calamagrostis spp., Betula pumila. Some hummock species were present also, of which Tomenthypnum nitens was confined to eutrophic situations, whereas Vaccinium and Ledum occurred throughout the areas in dry

microhabitats. In vegetation groups 4-8 hummocks covered small surface areas.

Bryophytes had a prominent part as indicators. Their importance could be attributed to the way vegetation analysis was carried out. Vegetation sampling took place between the end of May and the end of July, and there were numerous changes in the vascular plant layer, while the bryophytes were a permanent and recognizable part of the vegetation throughout the sampling season.

F. DECORANA- analyses

The scattergrams of plotting the first two axes of the DECORANA-ordinations for the NOTREES data set are presented in Figures 7, 8 and 10, with the corresponding TWINSpan-vegetation groups overlayed on each scattergram. Most of the vegetation groups could be delineated easily. Vegetation group 6 in Figure 8 demonstrated a case where the sites were widely apart and scattered within other groups inside the space created by the two axes.

An ecological interpretation of the scattergrams was obtained by correlating the sample scores of axis 1 (x) and axis 2 (y) of the ordinations with the measured water and peat properties for each sample site. Also, the x- and y-axis scores were averaged for each vegetation group and these values correlated with selected water, peat and tree cover properties for all sites and for Area I. Principally

the results showed that the information conveyed by DECORANA was equivalent to the TWINSpan- results, by way of the initial ordination of the latter analysis.

In the analysis of all sites (Figure 7), the x-axis scores had the strongest positive correlations with peat nitrogen ($r=0.750$, $n=57$), peat phosphorus ($r=0.611$, $n=57$), tamarack basal area ($r=0.417$, $n=63$) and peat depth ($r=0.413$, $n=49$). They were negatively correlated with peat C/N-ratio ($r=-0.620$, $n=57$) and black spruce basal area ($r=-0.464$, $n=111$). This axis had an eigenvalue of 0.50, accounting for 50 % of the variation. The correlations suggested a gradient of increasing nutrient richness along the first axis. The y-axis scores had negative correlations with peat nitrogen ($r=-0.407$, $n=57$) as well as water pH ($r=-0.396$, $n=55$) and conductivity ($r=-0.376$, $n=53$), indicating a trend of decreasing minerotrophy along the second axis. The second axis accounted for 31 % of the remaining variation. All correlations were significant at the 95 % level, but the corresponding r^2 -values derived from these individual sample scores did not account for much variation. When the x-axis scores were averaged for each vegetation group and these values correlated with the environmental data, r^2 -values were higher: for tamarack basal area, $r^2=0.753$, for total peat nitrogen $r^2=0.662$, for total peat phosphorus $r^2=0.489$ and for black spruce basal area $r^2=0.268$. The group averages of y-axis scores showed a r^2 -value of 0.515 for water pH and that of 0.252 for total peat nitrogen.

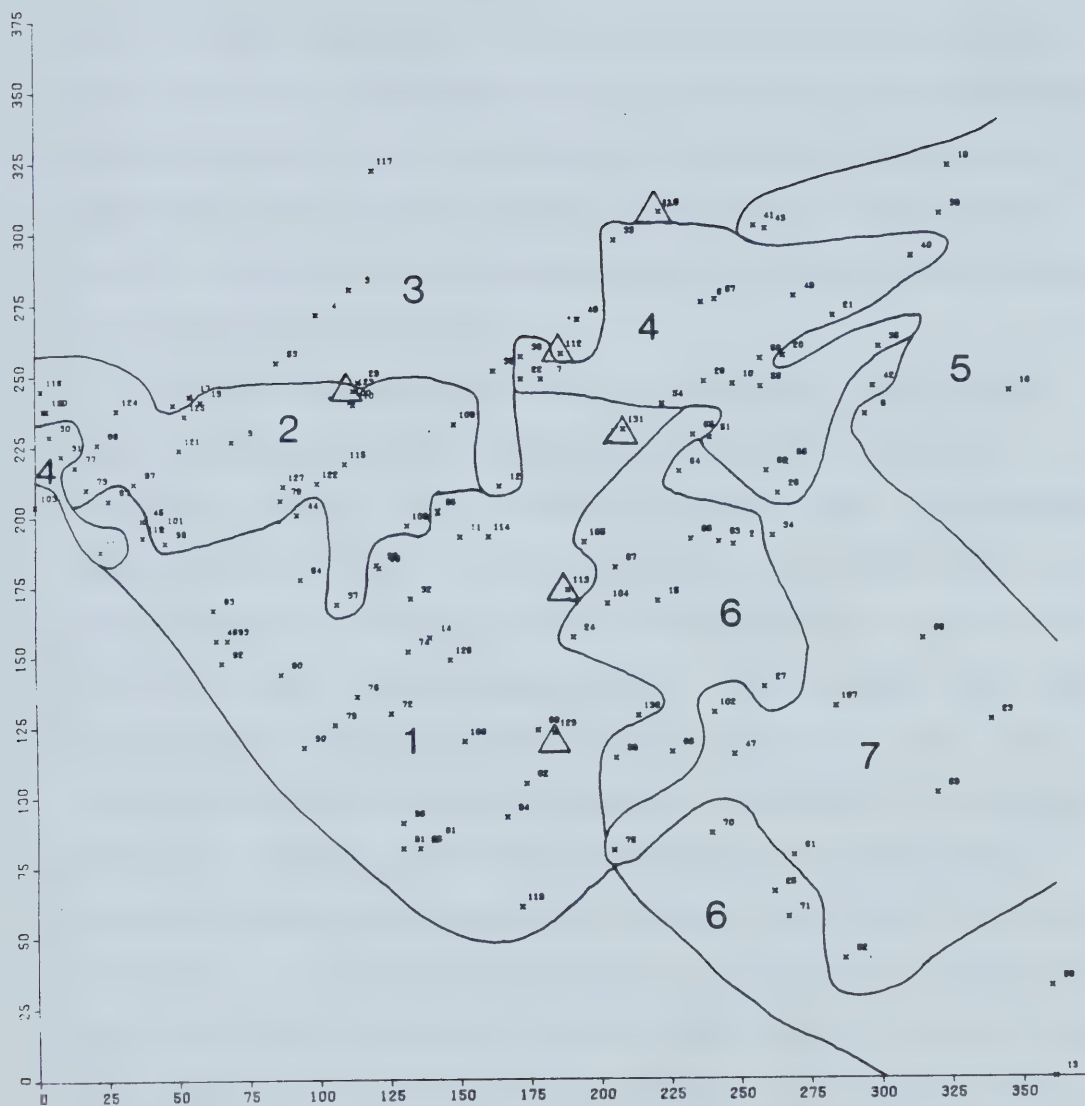


Figure 7. The sample sites plotted according to their scores on the first two axes of the DECORANA-analysis; all sites, NOTREES data set. The corresponding TWINS-SPAN-vegetation groups superimposed on the scattergram.

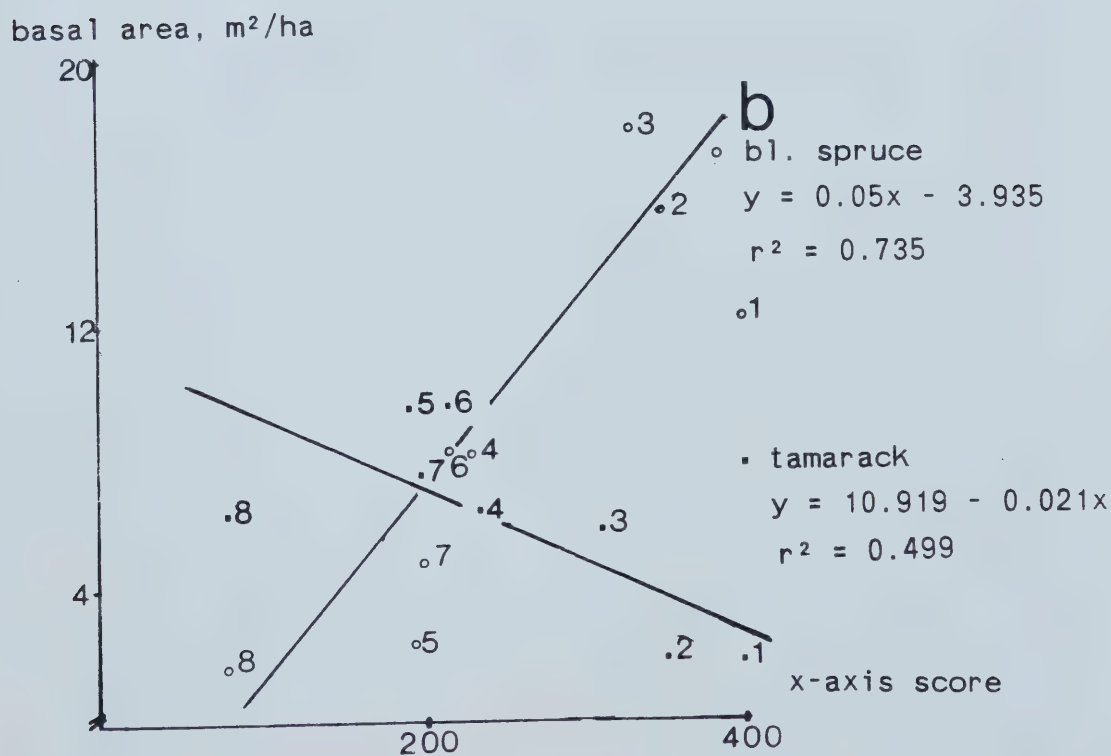
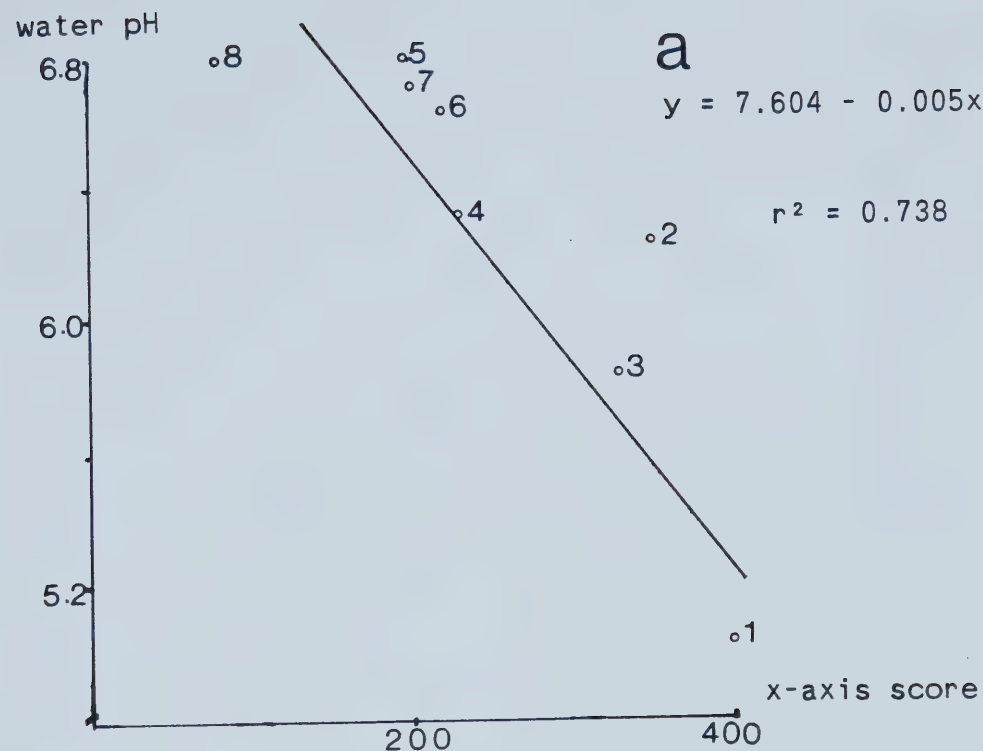
△ - white spruce sites (group 8).

The TWINSPAN-groups conveyed similar information. In Figure 7, vegetation groups 2 and 3 had a position in the upper left corner, which was a black spruce dominated area low in peat nutrients and minerotrophy. In earlier analysis these groups were the most oligotrophic and poor in nutrients. Opposed to them, in the lower right corner, were groups 6 and 7, a nutrient-rich tamarack area; this was also evident in the earlier analysis.

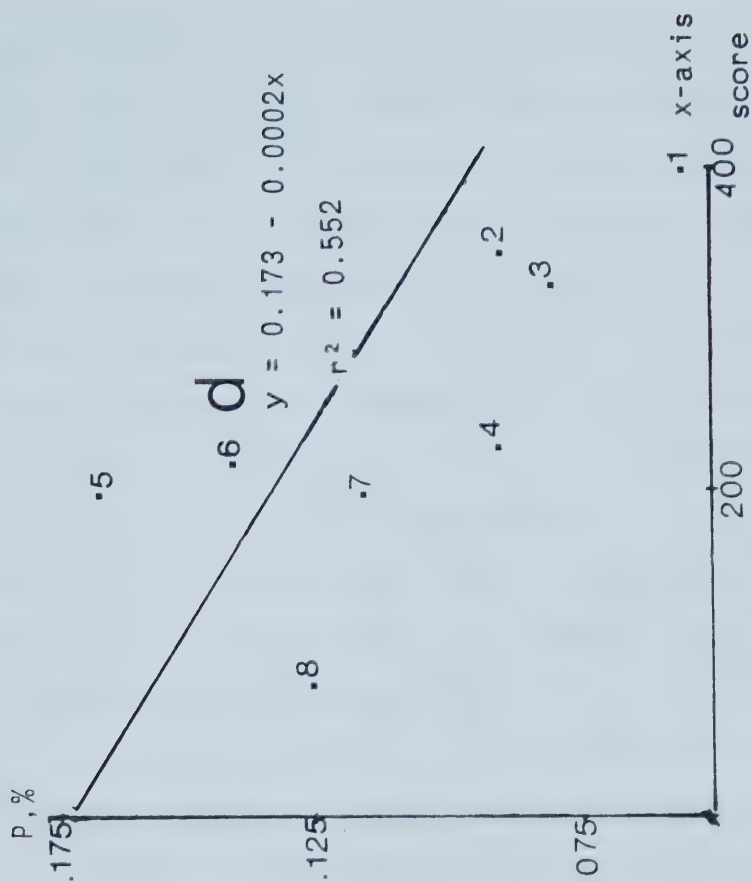
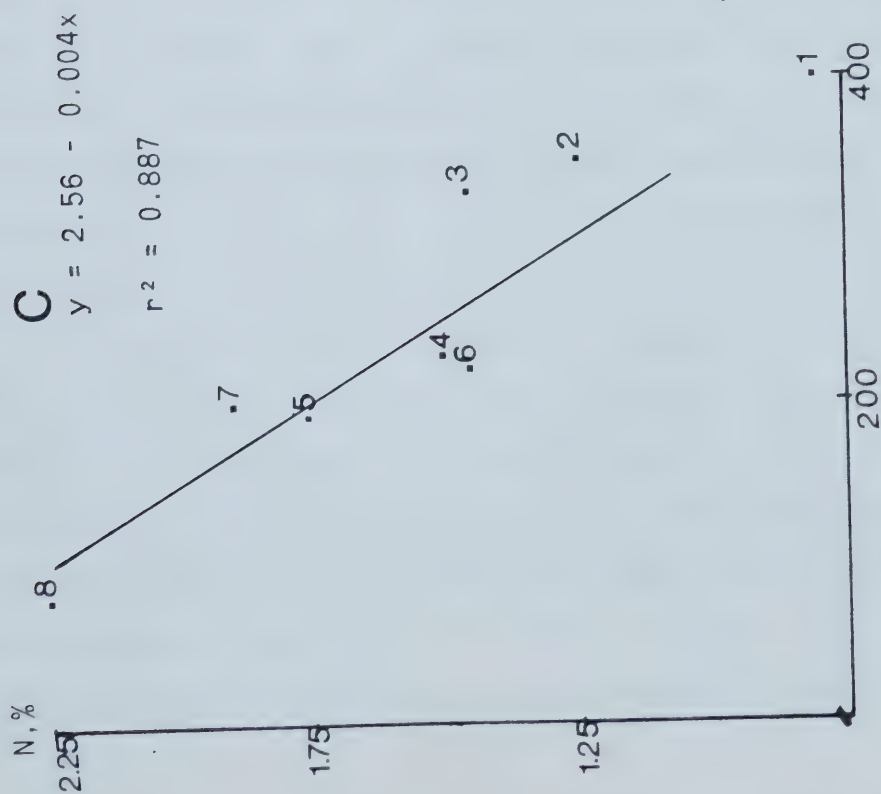
In the ordination of Area I (Figure 8), the x-axis scores were negatively correlated with peat nitrogen ($r=-0.815$, $n=37$), pH of water ($r=-0.683$, $n=38$) and tamarack basal area ($r=-0.687$, $n=53$). Positive correlations were with peat C/N-ratio ($r=0.682$, $n=37$) and black spruce basal area ($r=0.441$, $n=62$). The eigenvalue for the axis was 0.58, and the correlations were significant at the 95 % level. Thus increasing x-axis values suggested a decrease in nutrients and ionic content. Also here, averaging the axis score values for the eight vegetation groups accounted for more variation: r^2 -value for total peat nitrogen was 0.887, for water pH 0.738, for black spruce basal area 0.735, for total peat phosphorus 0.552 and for tamarack basal area 0.499 (Figures 9a-d). This finding confirmed the clear environmental gradient among the TWINSPAN-groups with Area I.



Figure 8. The sample sites plotted according to their scores on the first two axes of the DECORANA-analysis; Area I, NOTREES data set. The corresponding TWINSpan-vegetation groups superimposed on the scattergram.



Figures 9a-b. Correlations between the first axis DECORANA-scores of the TWINSpan-vegetation groups and their water pH (a) and black spruce and tamarack basal area values (b), Area I.



Figures 9c-d. Correlations between the first axis DECORANA-scores of the TWINSpan-vegetation groups and their total peat nitrogen (c) and phosphorus (d) values, Area I.

Correlations with the y-axis scores were weak; the highest was with peat depth ($r=0.174$, $n=30$), which was not significant at the 95 % level. However, the eigenvalue of this axis was 0.40, which indicated that there existed environmental variation which was not measured and which evidently spread the data in this direction. Correlating the averaged sample scores of the vegetation groups resulted in low r^2 -values: an r^2 -value of 0.177 for total peat nitrogen and that of 0.144 for total peat phosphorus.

In Figure 8, the feathermoss-black spruce-groups 1-3 were separated into a close entity, manifesting their vegetative homogeneity and dissimilarity from the other groups. These groups were poorest in nutrients on Area I and their high x-axis scores with the negative correlations supported this finding. Also the above mentioned division into black spruce versus tamarack dominated sites was confirmed by the correlations. On the other hand, the brown moss-tamarack-groups 4-7 covered large areas on the scattergram, showing their greater vegetative and environmental variation.

In the scattergram for Area II (Figure 10), there was no overlapping between the groups. Treeless sites were distinct outliers. The x-axis scores had strongest correlation with peat depth ($r=0.729$, $n=17$) and a negative one with electric conductivity ($r=-0.538$, $n=16$), both of which could be verified by the values of the TWINSpan-groups. They also were significant at the 95 %

level. The y-axis scores showed a slightly positive correlation with peat nitrogen ($r=0.440$) and phosphorus ($r=0.439$, $n=18$ for both). These correlations were not significant at the 95 % level. The eigenvalue of the x-axis was 0.41 and of the y-axis 0.29.

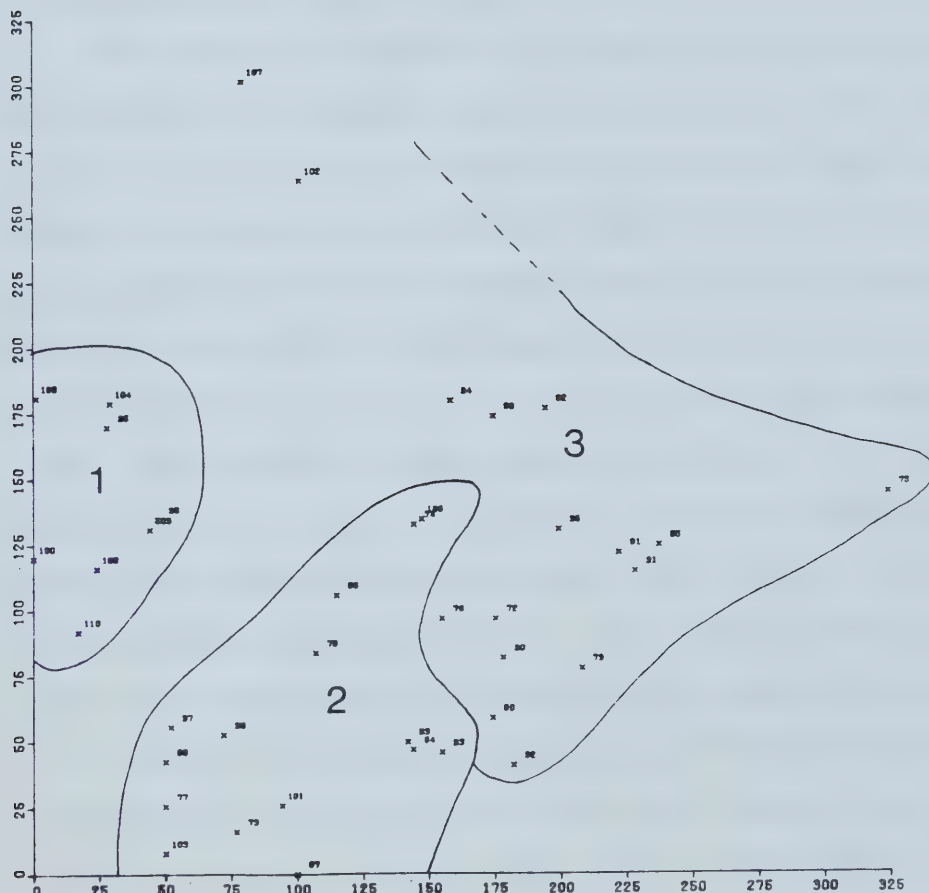


Figure 10. The sample sites plotted according to their scores on the first two axes of the DECORANA-analysis; Area II, NOTREES data set. The corresponding TWINSPLAN-vegetation groups superimposed on the scattergram.

G. Water table depth and hydraulic conductivity

Water table depth on area I varied from 0 cm (water at the surface) to 90 cm and was on the average 17 cm (Table 6a). The gradient from dry, hummocky sites to wetter, lawn- and hollow-dominated sites is evident from the water table data also. The tamarack-growing brown moss-characterized sites had water closest to the surface, and the black spruce - feathermoss- sites were typically drier.

The hydraulic conductivity, which on the average was measured at 84 cm depth, varied between 1.8×10^{-4} cm/s and 34.1×10^{-4} cm/s; the average was 10.2×10^{-4} cm/s ($n=28$) (Table 6a). Results by Gillard (1984)⁴ using the same method on the same area, at an average depth of 90 cm, were very similar. The range of hydraulic conductivity in Finnish peatlands is from 0.2×10^{-6} to 110×10^{-4} cm/s (Päivänen 1982). The values of these data were within this range, but higher than the values presented by Boelter (1965) for dense, decomposed herbaceous peat (0.075×10^{-4} cm/s) and undecomposed moss peats (0.381×10^{-4} cm/s). There were no distinct trends among the vegetation groups of these data.

Hydraulic conductivity decreases with advanced degree of decomposition of peat and even more sharply with increasing depth of measurement. The differences are primarily due to changes in the pore size distribution of peat (Boelter 1965). With advancing decomposition, there is a considerable decrease in the diameter of the pores and

⁴Personal communication: Discussion, Dec. 1984

water is held more tightly. Also, peat types differ in their conductivity qualities. Undecomposed moss peats contain more than 95 % water by volume in saturation and release 50 to 80 % of this water to drainage. Herbaceous peats may contain between 80 and 90 % water at saturation but yield only 10 to 15 % of this to drainage. Consequently, lowering the water table would drain little water from a decomposed peat but a great deal from an undecomposed peat (Walmsley 1977).

Values for the drainability of different peat types using their hydraulic conductivity as a discriminant have not been determined. The differences in the velocity of water movement can, however, be taken into account in the ditch spacing design of a drainage site. For example, treeless peatlands require a denser ditch network than forested peatlands, due to the woody and more permeable peats of the latter types (Heikurainen 1971a). On a more exact level, hydraulic conductivity measurements were used as a basis for theoretical calculations of ideal ditch spacing on the experimental drainage area near the Saulteaux River, and the results coincided very well with the ditch spacing guidelines used in forest drainage in Finland (Toth 1985)⁵.

⁵ Personal communication: Discussion, Feb. 1985

H. Peat fibre content

The unrubbed fibre content of peat can be used as an indicator of the degree of humification. According to the System of Soil Classification of Canada (1970), organic material is fibric if 67 % of the fibre content is larger than 0.15 mm, mesic if 33 - 67 %, and humic if less than 33 %. In these data, the overall average of 68.7 (± 17.8 , $n=15$) % fibre content larger than 0.15 mm places these peats into the fibric category. These values are not descriptive for drainage purposes, as the number of determinations was low and peat samples were taken from the surficial layers. On Area I, the range in peat fibre content was 47 - 83 % with an average of 71.2 ± 13.3 % ($n=9$), and on Area II 39 - 99 % with an average of 65.0 ± 23.9 ($n=6$) %.

I. Peat depth

Peat depth is an important factor when assessing the feasibility of drainage. Sites with shallow peat are generally the first stage in development from a mineral soil site to an organic site and are still influenced by the underlying mineral soils. Often they are not much different from the corresponding mineral sites and the slight peat accumulation does not impede forest growth. With deepening peat layers, the character of the site changes fundamentally and it becomes necessary to take forest improvement measures if forest growth on the site is desired. Peat depth alone is not decisive to the potential of the site for forest growth,

but it is an important source of variation and can be used in stratifying the data in analysis. The differences in peat depth in these data were taken into account in the separate analyses of the two areas, dividing between the deep peat area I and the shallow peat area II.

J. Peat chemistry

pH

Perhaps the most important parameter in peat nutrient status is pH, as it indicates overall nutrient availability. At lower pH-values peat is rich in H^+ -ions, with the saturation point being $pH=3.0$, and at high pH's peat is increasingly rich in Ca^{2+} -ions, with a saturation point of $pH=7.7-7.8$. Lucas and Davis (1961) state ideal pH-values for nutrient availability to be 5.0 in Sphagnum-peat and 5.5-5.8 in woody-sedge peat.

The peat pH-values in these data varied from 3.44 to 7.52. Lower values were rare, and the median values for the two main areas were 6.25 (range 3.44-6.74) and 7.05 (6.39-7.52), respectively. These values even exceed those mentioned above for ideal nutrient availability. This aspect will be discussed with each peat property separately.

Nitrogen

Nitrogen is the nutrient that for the largest part determines the level of productivity (Alexander 1978), in peatlands. An adequate supply of nitrogen is one of the most important factors determining the suitability for site improvement by drainage. Total nitrogen amounts in peat are usually high, but the bulk of nitrogenous materials is organic, plant residues and unavailable. With soil pH-values under 4.0, total nitrogen usually amounts for less than 1 % in the peat. When pH is over 5.0, nitrogen can exceed 2 %. Nitrogen contents required for sustained forest growth vary between 1.3 - 1.5 %. Holmen (1964) states that if the nitrogen content of peat is 1.3 % or over, the site can maintain a tree stand assuming other nutrients are adequate. Average nitrogen amounts in drainable spruce mires in Finland are 1.5 - 2.2 % and in pine mires 1.2 - 1.6 %, and nitrogen fertilization is recommended if peat contains less than 1.2 - 1.3 % nitrogen (Heikurainen 1979). Malmström (1956) refers to peatlands with nitrogen content of 2.0 - 2.5 % as 'remarkably nitrogen-rich'.

The amount of total peat nitrogen in the vegetation groups of the all sites-analysis (Tables 3a and 4a) ranged from 1.0 (± 0.42) % to 2.09 (± 0.16) %. The lowest values were in black spruce-growing vegetation groups characterized by Sph. fuscum, feathermosses, Ledum and Vaccinium vitis-idaea, and the highest values were in groups characterized by brown mosses, Sph. warnstorffii, Tomenthypnum and tamarack. The

former groups (nos. 1-3) were lower in nitrogen than is required for sustained forest growth, whereas all the latter groups (nos. 4-7) had an adequate nitrogen supply.

The division into poor vs. rich nitrogen sites was even sharper in the analysis for Area I (Tables 4a and 5a). The indicator species for vegetation groups 1-3 (NOTREES) or 1 and 2 (BASAL) - the same as in the feathermoss-groups of all sites-analysis - denoted sites with nitrogen contents between 0.78 - 1.33 %, with an average of 1.08 %; on the other hand, brown mosses, Betula pumila, Carex aquatilis, Tomenthypnum and Salix spp. were indicative of sites with nitrogen contents of 1.43 - 2.27 %, with an average of 1.77 %. The consistency of species division in this regard suggested that the border between insufficient vs. sufficient nitrogen content could be assessed by the presence of the latter species; areas dominated by Sph. fuscum, feathermosses and their associate species did not have adequate amounts of nitrogen for sustained forest growth after drainage.

On Area II the nitrogen values of vegetation groups varied between 1.24 - 1.41 %, thus bordering on insufficiency. A good portion of the peat samples from this area consisted of the remains of Sph. fuscum, an indicator of poor nutrient conditions. The dominance of this species on the minerotrophically rich Area II with a shallow peat layer was somewhat odd. The occurrence of Sph. fuscum-hummocks is not unusual on rich fens, however,

(Heikurainen 1953, Horton *et. al.* 1979) and their dominance has been found to decrease the value of eutrophic sites for forest growth. The results were from 20-26 years old drainage areas in Finland (Heikurainen 1957). In the Finnish peatland classification system, the eutrophic pine-growing peatlands are divided into two types according to the occurrence of Sph. fuscum-hummocks. Eutrophic pine swamps (terminology: Heikurainen and Pakarinen 1982) are characterized by an abundance of rich fen species, a strong shrub layer and hummocks growing Pleurozium schreberi and Hylocomium splendens. These sites belong to class I in the site quality classification as presented in Table 1 (Huikari 1974). The other type, eutrophic pine fens, also have a distinct rich fen vegetation, but frequent Sph. fuscum-hummocks drop them into class IV in the classification. For both site types, PK-fertilization is required in addition to drainage (Heikurainen 1978).

The ratio between soil carbon and nitrogen affects nutrient conditions. High C/N-ratios mean a lot of undecomposed material in the system and nitrogen becomes the limiting factor for growth. The average ratio in very acid soils is 60:1, in soils with about 2 % nitrogen it is 30:1 (Lucas and Davis 1961). In these data, the ratio is relatively favourable, around 30:1 on both study areas.

Plants assimilate nitrogen almost entirely in inorganic forms, as ammonium (NH_4^+) or nitrate (NO_3^-). The conversion of organic nitrogen to the inorganic forms, through

ammonification and nitrification processes, is affected by peat pH, moisture and aeration, temperature, C/N-ratio, nitrogen content of the soil. Ammonification occurs even in anaerobic, water-saturated conditions, but nitrification happens only in well-aerated habitats. The lower limit for nitrification is at pH:s 3.7 - 4.0, and anywhere below pH 5.0 there is a marked reduction in nitrification rates (Alexander 1978, Lucas and Davis 1961). In these data, the ratio of ammonium to nitrate in peat was on the average 20:1. Nitrate amounts were uniform through the data (average was $6.03 \pm 4.07 \mu\text{g/g}$, $n=58$) but ammonium amounts varied (average was $117 \pm 83.8 \mu\text{g/g}$, $n=58$). Their values or ratios did not show any trends between the vegetation groups.

Phosphorus

Phosphorus is second to nitrogen in importance for nutrients required by plants and micro-organisms. The amount of total phosphorus in peat varies from 0.01 % in very acid soils to over 0.05 % in soils well supplied with calcium (Lucas and Davis 1961). Phosphorus is found organically bound in peats and its availability is controlled by soil pH's. Soluble phosphates are efficiently tied up in mineral compounds, especially at high pH-levels. On pH-levels below 5.5, they can be tied up with iron, at levels between 3.0 - 7.0 with aluminium and at pH's greater than 6.0 with calcium. The ideal pH for phosphorus availability in peat is stated to be 5.5 (Lucas and Davis 1961). The experience from

drained peatlands has shown problems in phosphorus availability already at pH's greater than 4.8 (Heikurainen 1979).

According to Malmström (1956), peat phosphorus contents less than 0.045 - 0.090 % are possibly insufficient for forest growth. The average values for drainable spruce sites in Finland are 0.070 - 0.110 %; for pine sites the values are much lower, 0.030 - 0.050 % (Heikurainen 1979).

In the all sites- analyses of these data (Tables 3a and 4a), the group averages for total peat phosphorus were between 0.070 and 0.141 %. The feathermoss-groups were lower with an overall average of 0.080 %, whereas the value for the tamarack-brown moss- groups was on the average 0.120 %. Highest values were in the groups characterized by tamarack-black spruce mixed forest with Betula pumila and Sph. warnstorffii.

On Area I, the same trend was evident (Tables 5a and 6a). The feathermoss-side had significantly lower peat phosphorus values compared to the tamarack-brown moss-side. The division was on the average between groups with phosphorus contents of 0.075 % vs. 0.125 %. This difference is meaningful in assessing the adequacy of phosphorus supply, especially because the groups that were poor in phosphorus had, in general, insufficient amounts of nitrogen as well.

The values of peat phosphorus on Area II were on the borderline for sufficiency, as was the case with nitrogen

also (Table 7a).

No differences or trends among vegetation groups were found in the amounts of soluble phosphorus, PO_4^- .

The pH-values of peat exceeded those cited for ideal availability. There is evidence that high peat pH-levels may affect the availability of phosphorus and render such sites less suitable for forest drainage (Heikurainen 1959, 1982).

Potassium

The amount of potassium is usually low in organic soils. Potassium is found in mineral forms; it is not known to enter the structure of organic compounds (Armson 1977). Lucas and Davis (1961) report very acid organic soils with less than 0.1 % potassium, and soils with high calcium content having approximately 0.15 % potassium. These levels are higher than the 0.085 % reported by Malmström (1956) as the minimum level of potassium to support continuous forest growth. The discrepancy in the amounts may be due to expressing potassium as K_2O by Lucas and Davis (1961), namely 0.085 % K is equivalent to 0.1 % K_2O . Drainable spruce sites in Finland have on the average 0.03 - 0.07 % and drainable pine sites 0.03 - 0.05 % potassium (Heikurainen 1979).

In these data, the potassium values exceeded minimum levels required for drainability, but did not generally equal the 0.085 % limit. The overall average was 0.062 ($\pm$ 0.031, $n=57$) %, and the averages on Areas I and II 0.069 ($\pm$

0.030, n=37) and $0.038 (\pm 0.016, n=18) \%$, respectively. The 'drier' area II was lower in peat potassium than Area I with its wetter conditions.

Exchange capacities and calcium content

The cation exchange capacity (CEC) of peat expresses the total amount of major positive charges or cations adsorbed by the peat. The higher the capacity, the more nutrients the peat can store. CEC increases with the dryness and higher calcium concentrations of peat. Sphagnum-peats have higher values than sedge peats, and the highest exchange capacity values are recorded in eutrophic Sphagnum-Carex-peats, since they contain both moderate concentrations of calcium and a large proportion of Sph. fuscum (Puustjärvi 1956). Total exchange capacity (TEC) expresses the amount of all exchangeable ions in the soil, including H^+ -ions. Base saturation is used to measure the trophic status of peat. It indicates the percentage fraction of basic cations Ca^{2+} , Mg^{2+} , Na^+ and K^+ of the TEC (Walmsley 1977). Base saturation was high on the study areas, averaging about 80 %.

CEC and TEC values in these data compared well with the ranges cited by Walmsley (1977) of 131 - 200 meq/100 g for moss-dominated peats and 100 - 192 meq/100 g for sedge-dominated peats. There were no significant differences in either CEC or TEC between the vegetation groups. Higher values on Area II ($CEC\ 136 \pm 35, n=15$, vs. $100 \pm 23, n=37$ on

Area I) were due to the abundance of dry Sph.
fuscum-hummocks.

Of the cations composing the exchange capacity, calcium is most often used as an indicator of eutrophy. Together with peat pH and nitrogen, it reflects overall fertility. In these data, the calcium content of peat was over 1.5 % on both study areas, manifesting the calcareous bedrocks of the study areas and their surroundings. For comparison, drainable sites in the granite-dominated Finland have on the average 0.50 - 1.07 % (spruce sites) to 0.43 - 0.79 % (pine sites) calcium content (Heikurainen 1979).

IV. Conclusions

This pilot study was relatively successful in answering the objectives stated for it. Given the uniformity between the study sites and the narrow environmental variation, the TWINSpan-method in vegetation analysis gave satisfactory results. There were differences among the sites in regard to their potential for forest growth after drainage, and the vegetation was indicative of them to a satisfactory degree. A gradient reflecting differences in the amounts of peat macronutrients was especially well demonstrated among the vegetation groups on Area I. Combining the TWINSpan-results and the water and peat data, sites that had potential for sustained forest growth after drainage could be separated from those that did not, using indicator species. Picea mariana sites dominated by Sphagnum fuscum, Pleurozium schreberi, Hylocomium splendens, Ledum groenlandicum and Vaccinium vitis-idaea had peat nitrogen and phosphorus contents which, in the light of available literature, were considered inadequate for continuous forest growth without added nutrients. The occurrence of Plagiomnium ellipticum, Brachythecium turgidum, Drepanocladus spp., Calliergon spp., Sphagnum warnstorffii, Tomenthypnum nitens, sedge species as Carex aquatilis and Carex diandra, indicated conditions where peat nutrient levels should be sufficient to sustain forest growth. These results were in agreement with numerous other investigations carried out in peatland forestry (see e.g. Jeglum *et al.* 1974, Heikurainen 1979).

stratification of sampling on a site, paying special attention to the various microtopographical surfaces, would have given insight into the patterning and development of these areas. As it was carried out, the sampling had more the character of a forest inventory than that of a vegetation study. The randomness of the vegetation data was realized and accounted for in the analysis, e.g. by downweighing rare species in the DECORANA-ordinations. Still, as far as answering the objectives of the study, the essential characters in the vegetation were captured.

This pilot study gave insight into further forestry-oriented peatland investigations. To obtain a classification that would be applicable to a large area, it would be desirable to cover a wide geographical range (e.g. the areas of distribution of black spruce and tamarack in the boreal zone) with tree stands varying in their composition and developmental stage. A few large tree-vegetation-peat and water sample plots could be descriptive of an entire homogenous peatland, and the level of detail could be increased with the requirements of individual operations. Also, accomodating the investigation to the Canadian Wetland Classification System with its four levels (wetland classes, forms, types and varieties) (Zoltai and Pollett 1983) would be useful.

Peatland drainage has been carried out with satisfactory results on areas poorer in overall nutrient status than the areas in this study. Site improvement on

ombro- or oligotrophic sites is not impossible but it requires high intensity management, particularly fertilization to compensate for nutrient deficiencies. Sites with severe nitrogen deficiency should especially be excluded from any drainage activity, as the costs of nitrogen fertilization exceed the limits of a reasonable investment. Fertilization with phosphorus and potassium is used to increase the growth and value of the stands, but there should be a naturally adequate nitrogen supply on the site. Generally, the more nutrient-rich the site is in the natural condition, the better the tree growth and the larger the recoverable merchantable volume after drainage (Stanek 1977b). However, it is exactly the rich fen- character of the sites in this study that adds complexity to the predictions of drainage effects. The experience from draining sites with corresponding levels of peat pH and calcium in Fennoscandia, relatively rare as these sites there are, has shown poor results. There are examples of seeded pine stands on eutrophic mires that have grown well for the first 15-20 years but whose development has stopped unexpectedly (Heikurainen 1959). The most probable reason for this is the special nutrient status of eutrophic mires. Malmström (1956) states that to grow forests on calcium-rich mires (kalkmyrar), fertilization with potassium or phosphorus, or both, is needed. This has been the recommendation in Finland also (Heikurainen 1978). Later research has shown complications in peat micronutrient

contents and ratios as well (Heikurainen and Pakarinen 1982). For these reasons, and for the fact that there have been large areas of forested moderately nutrient-rich peatlands to work on, rich fens are completely excluded from drainage in Finland today. This situation is reinforced by the demand for conservation of these exceedingly rare peatland types.

The examples of drainage results in this thesis were mainly from Fennoscandia, as forest drainage has not been practiced on a large scale in Canada. The differences in climatic conditions and tree species make predictions for Alberta, based on Finnish data, somewhat tentative. For example, the accumulated temperature sum, one of the major variables when assessing the post-drainage forest growth on peatlands, is much higher in Alberta (2000+ degree days (d.d.) (Atlas of Alberta 1969), compared to 800 - 1400 d.d. in Finland). Higher temperature sums make the situation more favourable by potentially faster decomposition of organic material and nutrient cycling.

The results of the several drainage experiments recently conducted or planned in Alberta (Hillman 1984) will yield valuable information for decision-making. Experimental data for local conditions are necessary in deciding the feasibility of expanding forestry operations to organic sites in Alberta as one measure to increase productive forest land base.

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VI. Appendices 1-7

Appendix 1. Means and standard deviations of water and peat parameters (median values and ranges for water and peat pH) on the study areas. (Sample size for each mean in brackets.)

AREA	I	II	III
# of sample sites	71	39	21
water properties:			
pH	6.4 (4.1-7.2) (38)	7.0 (6.6-7.5) (13)	6.2 (4.0-7.0) (7)
cond., μ S	111 $\pm$ 38.4 (36)	200 $\pm$ 38.9 (13)	90 $\pm$ 83.1 (7)
Ca, ppm	20 $\pm$ 7.7 (42)	57 $\pm$ 11.4 (13)	28 $\pm$ 29.3 (7)
Mg, ppm	5.2 $\pm$ 1.8 (42)	12.8 $\pm$ 2.5 (13)	5.1 $\pm$ 4.6 (7)
Na, ppm	5.5 $\pm$ 3.5 (42)	0.1 (13)	0.1 (7)
K, ppm	0.7 $\pm$ 1.1 (42)	0.1 (13)	0.1 (7)
peat properties:			
pH	6.2 (3.4-6.7) (37)	7.0 (6.4-7.5) (15)	5.8 (3.8-7.0) (7)
total C, %	45 $\pm$ 2.9 (37)	38 $\pm$ 6.2 (15)	45 $\pm$ 2.3 (7)
total N, %	1.65 $\pm$.5 (37)	1.31 $\pm$.5 (15)	1.26 $\pm$.3 (7)
NH ₄ , μ g/g	113 $\pm$ 67 (37)	145 $\pm$ 121 (15)	82 $\pm$ 37 (7)
NO ₃ , μ g/g	6.2 $\pm$ 3.0 (37)	6.5 $\pm$ 6.4 (15)	4.2 $\pm$ 1.3 (7)
C/N	30 $\pm$ 12 (37)	32 $\pm$ 10 (15)	39 $\pm$ 13 (7)
total P, %	.117 $\pm$.04 (37)	.086 $\pm$.03 (15)	.090 $\pm$.02 (7)
PO ₄ , μ g/g	33 $\pm$ 27.9 (37)	31 $\pm$ 16.7 (15)	31 $\pm$ 17.3 (7)
Ca, %	1.62 $\pm$.42 (37)	2.34 $\pm$.6 (15)	1.52 $\pm$.9 (7)
K, %	.069 $\pm$.03 (37)	.038 $\pm$.02 (15)	.086 $\pm$.002 (7)
CEC, meq/100 g	100 $\pm$ 23 (37)	136 $\pm$ 35 (15)	90 $\pm$ 47 (7)
TEC, " base	129 $\pm$ 25 (37)	159 $\pm$ 35 (15)	139 $\pm$ 42 (7)
saturation	79 $\pm$ 22.6 (37)	85 $\pm$ 8.6 (15)	63 $\pm$ 21.7 (7)
ash, %	12.9 $\pm$ 5.6 (37)	18.1 $\pm$ 7.5 (14)	12.0 $\pm$ 4.3 (7)
depth, cm	121 $\pm$ 38 (30)	56 $\pm$ 22 (14)	89 $\pm$ 45 (7)
tree species, basal area, m ² /ha:			
bl. spruce	7.6 $\pm$ 7.8 (71)	11.3 $\pm$ 6.5 (39)	-
tamarack	5.8 $\pm$ 6.1 (71)	-	-

Appendix 2. Means and standard deviations of the water and peat properties and tree cover of the TWINSpan-vegetation groups; all sites, NOTREES data set

vegetation group	(8)	1	2	3	4	5	6	7
# of sites	6	28	26	14	21	6	18	12
location								
area I		14 %	15 %	86 %	100 %	100 %	83 %	75 %
area II		71 %	46 %				17 %	25 %
area III	100 %	14 %	38 %	14 %				
water properties:								
pH	6.59 ± .34	7.02 ± .32	6.18 ± 1.38	5.75 ± -	6.74 ± .23	6.11 ± .57	6.82 ± .18	6.79 ± .21
cond. µS	74 ± 35.1	204 ± 56.5	139 ± 81.9	71 ± 29.8	120 ± 31.6	108 ± 6.4	114 ± 30.9	152 ± 53.0
Ca, ppm	24 ± 8.5	59 ± 20.5	38 ± 24.3	16 ± 6.2	21 ± 5.3	19 ± 11.8	18 ± 5.1	32 ± 19.1
Mg, ppm	5 ± 1.5	13 ± 3.6	8 ± 5.1	4 ± 1.4	6 ± 1.2	6 ± 2.5	5 ± 1.4	8 ± 3.7
Na, ppm	.1 ± -	.6 ± 1.3	1 ± 2.6	3 ± 3.2	7 ± 2.0	6 ± 7.4	7 ± 4.2	4 ± 2.2
K, ppm	.1 ± -	.2 ± .4	.4 ± .9	.6 ± .7	.5 ± .4	.5 ± .8	1.3 ± 2.3	.2 ± .1
peat properties:								
pH	6.18 ± .31	6.82 ± .52	5.92 ± 1.66	5.80 ± .90	6.29 ± .24	6.31 ± .17	6.25 ± .17	6.45 ± .34
C, %	43 ± 1.8	40 ± 8.0	43 ± 3.4	44 ± 6.0	45 ± 1.9	46 ± 2.0	46 ± 1.0	44 ± 4.1
N, %	1.50 ± .11	1.27 ± .33	1.04 ± .42	1.24 ± .31	1.55 ± .29	1.58 ± .52	2.05 ± .27	2.03 ± .23
NH ₄ , µg/g	108 ± 23.1	90 ± 66.6	125 ± 101.1	74 ± 41.5	177 ± 53.9	116 ± 119	62 ± 28.2	148 ± 116.6
NO ₃ , µg/g	5 ± 1.5	7 ± 6.9	5 ± 2.3	5 ± 1.8	8 ± 4.3	5 ± 2.1	5 ± 2.1	5 ± 2.9
C/N	29 ± 3.2	32 ± 5.1	48 ± 21.0	36 ± 6.8	30 ± 5.4	31 ± 8.9	23 ± 3.0	22 ± 3.2
P, %	.111 ± .004	.085 ± .022	.070 ± .018	.084 ± .023	.141 ± .044	.090 ± .028	.118 ± .016	.134 ± .037
P0 ₄ , µg/g	20 ± 20.4	23 ± 16.3	43 ± 11.3	35 ± 23.6	43 ± 36.3	52 ± 44.6	25 ± 14.7	20 ± 13.5
Ca, %	2.0 ± .2	1.2 ± .7	1.6 ± .7	1.7 ± .8	2.3 ± .5	0.9 ± .5	1.8 ± .9	1.3 ± .6
K, %	.07 ± .01	.05 ± .03	.06 ± .03	.06 ± .03	.09 ± .02	.03 ± .02	.07 ± .04	.05 ± .02
CEC, meq/100g	116 ± 8.6	141 ± 28.4	94 ± 33.7	94 ± 33.7	97 ± 12.0	115 ± 13.7	95 ± 10.1	109 ± 16.9
TEC, meq/100g	160 ± 9.9	166 ± 33.6	132 ± 41.1	124 ± 21.0	130 ± 24.8	151 ± 29.0	120 ± 30.0	133 ± 21.2
base sat.	73 ± 4.9	86 ± 11.6	67 ± 31.2	76 ± 27.7	78 ± 18.0	77 ± 7.6	83 ± 21.6	84 ± 20.0
depth, cm	107 ± 51	51 ± 26	93 ± 33	97 ± 52	126 ± 31	95 ± 7	150 ± -	109 ± 47
tree species, ba m ² /ha:								
b1, spruce	4.5 ± 3.5	16.5 ± 3.2	7.0 ± 2.0	15.5 ± 7.7	5.5 ± 1.8	11.4 ± 2.2	1.2 ± 0.9	2.1 ± 1.3
tamarack	1.9 ± 3.0	.4 ± 1.1	.5 ± .8	2.3 ± 2.0	9.0 ± 3.0	6.7 ± 5.2	5.0 ± 3.2	6.1 ± 3.7
wh. spruce	3.6 ± 4.0							

Appendix 3. Means and standard deviations of the water and peat properties and tree cover of the TWINSpan-vegetation groups; all sites, BASAL data set

vegetation group	(8)	1	2	3	4	5	6	7
# of sites	5	21	28	23	18	8	16	12
location								
area I		5 %	14 %	74 %	100 %	100 %	87 %	85 %
area II		81 %	50 %	13 %			13 %	15 %
area III	100 %	14 %	36 %	13 %				
water properties:								
pH	6.55 ± .47	7.02 ± .32	6.25 ± 1.33	5.89 ± .93	6.85 ± .21	6.14 ± .52	6.80 ± .11	6.79 ± .21
cond., µs	75 ± 49.5	204 ± 56.5	128 ± 77.5	79 ± 32.3	123 ± 34.3	119 ± 8.9	109 ± 35.8	152 ± 53.0
Ca, ppm	25 ± 12.0	59 ± 20.5	35 ± 24.3	18 ± 7.3	20 ± 5.5	20 ± 10.4	19 ± 5.4	32 ± 19.1
Mg, ppm	4 ± 2.1	13 ± 3.6	8 ± 5.0	5 ± 2.2	5 ± 1.5	6 ± 2.0	5 ± 1.5	8 ± 3.7
Na, ppm	.1 ± .0	.6 ± 1.3	2 ± 3.3	3 ± 2.9	6 ± 2.0	7 ± 6.2	6 ± 4.5	4 ± 2.2
K, ppm	.17 ± -	.2 ± .4	.5 ± .9	.5 ± .6	.5 ± .5	.6 ± .7	1 ± 2.5	.2 ± .1
peat properties:								
pH	6.11 ± .40	6.88 ± .49	6.00 ± 1.49	5.89 ± .80	6.26 ± .25	6.30 ± .19	6.28 ± .20	6.45 ± .34
C, %	42 ± 2.3	39 ± 8.2	43 ± 3.5	44 ± 5.0	45 ± 1.9	47 ± 1.9	46 ± 1.2	44 ± 4.1
N, %	1.50 ± .16	1.27 ± .35	1.12 ± .42	1.25 ± .28	1.64 ± .32	1.60 ± .39	2.06 ± .30	2.03 ± .23
NH ₄ , µg/g	121 ± 3.4	88 ± 69.6	114 ± 93.9	87 ± 50.9	156 ± 74.9	176 ± 81.1	71 ± 42.9	148 ± 116.6
NO ₃ , µg/g	4 ± 1.9	8 ± 7.3	5 ± 2.0	5 ± 1.7	9 ± 4.7	6 ± 1.7	5 ± 2.1	5 ± 2.9
C/N	29 ± 4.5	32 ± 5.3	45 ± 19.9	36 ± 6.5	29 ± 5.8	30 ± 5.9	23 ± 3.4	22 ± 3.2
P, %	.113 ± .001	.083 ± .022	.075 ± .020	.090 ± .031	.142 ± .048	.100 ± .019	.125 ± .018	.134 ± .037
P0 ₄ , µg/g	13 ± 9.5	20 ± 13.1	41 ± 10.8	45 ± 30.6	32 ± 27.6	55 ± 47.6	26 ± 14.0	20 ± 13.5
Ca, %	2.0 ± .23	2.5 ± .5	1.6 ± 1.0	1.6 ± .6	1.5 ± .24	1.7 ± .31	1.6 ± .18	1.8 ± .32
K, %	.07 ± .01	.04 ± .03	.06 ± .03	.06 ± .03	.09 ± .03	.06 ± .03	.07 ± .03	.05 ± .02
CEC, meq/100g	115 ± 11.9	144 ± 28.3	98 ± 55.2	97 ± 30.9	95 ± 12.8	106 ± 15.2	99 ± 10.1	109 ± 16.9
TEC, meq/100g	154 ± 4.4	167 ± 35.1	135 ± 40.9	127 ± 31.1	125 ± 28.2	136 ± 21.0	134 ± 22.4	133 ± 21.2
base sat.	75 ± 5.6	87 ± 11.7	69 ± 28.4	79 ± 28.0	79 ± 22.1	78 ± 4.8	75 ± 11.3	84 ± 20.0
depth, cm	135 ± 21	51 ± 26	94 ± 38	98 ± 48	123 ± 34	113 ± 32	150 ± -	109 ± 47
tree species, basal area m ² /ha:								
b1, spruce	1.7 ± 1.6	16.2 ± 3.7	5.8 ± 2.0	16.7 ± 7.0	5.2 ± 5.3	11.2 ± 5.6	0.5 ± 0.5	2.2 ± 1.3
tamarack	1.7 ± 0.4	0.5 ± 1.3	0.3 ± 0.5	1.6 ± 1.9	10.1 ± 2.5	7.6 ± 3.1	4.7 ± 3.2	6.1 ± 3.7
wh. spruce	9.8 ± 5.5							

Appendix 4. Means and standard deviations of the water and peat properties and tree cover of the TWINSpan-vegetation groups; Area I, NOTREES data set

vegetation group	1	2	3	4	5	6	7	8
# of sites	5	9	8	6	14	5	14	10
water properties:								
pH	5.06 ± 1.35	6.25 ± .69	5.72 ± .95	6.30 ± .69	6.79 ± .10	6.66 ± .76	6.68 ± .05	6.82 ± .12
cond., μS	55 ± 20.5	80 ± 21.7	73 ± 38.2	116 ± 10.2	124 ± 33.4	153 ± 38.9	118 ± 14.8	123 ± 51.9
Ca, ppm	12 ± 11.3	21 ± 6.4	13 ± 5.7	20 ± 10.2	22 ± 6.2	21 ± 8.1	18 ± 4.2	21 ± 10.1
Mg, ppm	3 ± 2.4	6 ± 2.1	3 ± 1.3	6 ± 2.2	6 ± 1.3	5 ± 1.1	5 ± 1.2	5 ± 2.1
Na, ppm	5 ± 4.0	4 ± 3.2	3 ± 2.0	8 ± 6.0	6 ± 1.3	3 ± 3.3	8 ± 4.3	5 ± 2.4
K, ppm	2 ± 1.3	.7 ± .6	.5 ± .8	.7 ± .8	.3 ± .4	.4 ± .4	1.7 ± 2.7	.3 ± .4
peat properties:								
pH	4.85 ± 1.99	6.23 ± .42	5.96 ± .72	6.30 ± .16	6.28 ± .33	6.27 ± .02	6.28 ± .11	6.38 ± .27
C, %	45 ± 3.8	44 ± 7.1	46 ± 2.6	46 ± 2.2	45 ± 1.3	45 ± 2.0	46 ± 1.2	47 ± .9
N, %	.78 ± .37	1.25 ± .31	1.43 ± .08	1.50 ± .41	1.75 ± .32	1.47 ± .25	1.88 ± .23	2.24 ± .17
NH ₄ , μg/g	50 ± 21.1	81 ± 46.6	98 ± 17.3	110 ± 79.0	182 ± 43.2	184 ± 128.3	88 ± 59.9	67 ± 16.4
NO ₃ , μg/g	5 ± 2.2	5 ± 1.4	6 ± 1.3	6 ± 1.8	8 ± 4.9	8 ± 4.6	6 ± .9	5 ± 3.2
C/N	67 ± 36.3	36 ± 5.2	32 ± 2.7	32 ± 7.0	26 ± 5.6	31 ± 3.8	25 ± 3.4	21 ± 1.8
P, %	.054 ± .009	.088 ± .026	.082 ± .005	.090 ± .015	.163 ± .043	.141 ± .021	.117 ± .019	.124 ± .014
P0 ₄ , μg/g	37 ± 23.1	30 ± 15.6	54 ± 35.0	62 ± 49.6	18 ± 11.7	14 ± .01	38 ± 28.9	24 ± 12.9
Ca, %	1.2 ± 1.5	1.8 ± .4	1.6 ± .5	1.8 ± .3	1.7 ± .4	1.5 ± .3	1.5 ± .3	1.6 ± .2
K, %	.06 ± .03	.07 ± .02	.05 ± .02	.06 ± .04	.07 ± .03	.05 ± .1	.09 ± .04	.07 ± .02
CEC, meq/100g	69 ± 84.7	108 ± 21.5	97 ± 23.9	110 ± 13.7	104 ± 18.8	92 ± 15.7	96 ± 12.1	98 ± 12.6
TEC, meq/100g	118 ± 30.2	124 ± 18.4	148 ± 28.5	148 ± 19.2	138 ± 12.8	100 ± -	115 ± 36.2	120 ± 36.2
base sat.	51 ± 58.8	90 ± 26.6	65 ± 7.7	74 ± 3.1	75 ± 9.2	92 ± 15.7	90 ± 29.6	85 ± 25.9
depth, cm	90 ± 84.9	95 ± 37.0	130 ± 34.6	125 ± 28.9	121 ± 34.4	150 ± -	150 ± -	130 ± 34.6
tree species, basal area m ² /ha:								
b1, spruce	11.9 ± 5.2	15.5 ± 9.0	17.2 ± 7.2	8.2 ± 4.2	4.7 ± 2.0	7.7 ± 4.9	2.1 ± 0.9	1.5 ± 1.6
tamarack	1.8 ± 1.0	1.4 ± 1.6	5.0 ± 3.1	5.9 ± 4.6	8.8 ± 2.5	9.5 ± 5.3	7.3 ± 4.0	6.1 ± 2.2

Appendix 5. Means and standard deviations of the water and peat properties and tree cover of the TWINSpan-vegetation groups; Area I, BASAL data set

vegetation group	1	2	3	4	5	6	7
# of sites	5	12	14	9	11	8	12
water properties:							
pH	5.59 ± 1.07	6.14 ± .77	5.95 ± .52	6.69 ± .28	6.90 ± .19	6.67 ± .06	6.82 ± .11
cond, μ S	65 ± 26.8	82 ± 30.1	112 ± .	106 ± 15.1	128 ± 30.2	126 ± 12.2	129 ± 51.3
Ca, ppm	16 ± 8.1	18 ± 8.0	19 ± 13.6	17 ± 2.0	22 ± 4.9	20 ± 4.6	23 ± 10.0
Mg, ppm	4 ± 1.7	5 ± 2.5	6 ± 2.8	5 ± .5	6 ± 1.2	5 ± 1.6	5 ± 2.0
Na, ppm	4 ± 3.3	4 ± 1.6	6 ± 8.5	8 ± 1.9	6 ± 1.4	8 ± 6.0	6 ± 2.0
K, ppm	1 ± 1.1	.5 ± .7	.7 ± .9	.8 ± .6	.4 ± .4	2.3 ± 3.6	.2 ± .3
peat properties:							
pH	5.42 ± 1.38	6.15 ± .53	6.33 ± .24	6.25 ± .11	6.33 ± .27	6.26 ± .27	6.35 ± .33
C, %	42 ± 7.3	46 ± 1.9	47 ± 1.6	46 ± 2.0	44 ± 1.1	46 ± 1.5	46 ± 1.3
N, %	95 ± .44	1.33 ± .14	1.82 ± .45	1.58 ± .20	1.60 ± .34	1.97 ± .16	2.20 ± .18
NH ₄ , μ g/g	69 ± 50.8	83 ± 34.3	159 ± 131.7	139 ± 87.2	167 ± 57.3	75 ± 55.2	88 ± 42.7
N03, μ g/g	4 ± 1.8	6 ± 1.0	5 ± .5	6 ± .6	9 ± 5.0	5 ± .9	5 ± 2.0
C/N	51 ± 27.9	35 ± 3.9	27 ± 5.8	30 ± 3.6	29 ± 6.3	23 ± 2.6	21 ± 1.8
P, %	.070 ± .035	.082 ± .009	.100 ± .032	.132 ± .051	.152 ± .044	.112 ± .004	.127 ± .015
P04, μ g/g	30 ± 15.6	56 ± 35.7	25 ± 1.3	43 ± 42.2	21 ± 14.6	39 ± 40.0	21 ± 12.6
Ca, %	1.4 ± 1.0	1.8 ± .4	1.8 ± .4	1.5 ± .1	1.6 ± .2	1.6 ± .3	1.7 ± .3
K, %	.06 ± .02	.06 ± .03	.04 ± .02	.10 ± .03	.08 ± .02	.07 ± .04	.06 ± .03
CEC, meq/100g	84 ± 55.5	108 ± 20.2	113 ± 18.9	93 ± 8.3	100 ± 13.5	97 ± 16.3	105 ± 18.3
TEC, meq/100g	116 ± 21.1	147 ± 25.1	141 ± 33.3	106 ± 24.6	133 ± 15.3	140 ± 15.7	129 ± 27.1
base sat.	71 ± 48.8	75 ± 18.2	81 ± 5.7	92 ± 23.6	76 ± 13.0	69 ± 8.0	85 ± 22.1
depth, cm	83 ± 49.9	114 ± 33.6	90 ± .	150 ± .	83 ± 50	114 ± 34	90 ± 25
tree species, basal area m ² /ha:							
b1, spruce	14.1 ± 6.4	18.7 ± 5.8	11.4 ± 2.4	4.2 ± 1.3	4.7 ± 1.4	0.9 ± .5	1.6 ± 1.5
tamarack	1.5 ± 1.3	2.9 ± 3.1	8.0 ± 4.5	7.0 ± 2.2	8.7 ± 2.5	6.7 ± 5.1	7.1 ± 2.4

Appendix 6. Means and standard deviations of the water and peat properties and tree cover of the TWINSpan-vegetation groups; Area II, both data sets

vegetation group	1	2	3
# of sites	6	16	17
water properties:			
pH	6.49 ± .25	7.07 ± .30	7.18 ± .29
cond, μ S	64 ± 19.8	198 ± 28.0	214 ± 14.1
Ca, ppm	21 ± 5.4	55 ± 14.3	60 ± 2.8
Mg, ppm	4.5 ± .7	12 ± 2.6	14 ± .6
Na, ppm	4 ± 5.0	2 ± 5.0	.1 ± -
K, ppm	.6 ± .7	.1 ± 2.4	.1 ± -
peat properties:			
pH	6.04 ± .69	6.98 ± .50	6.95 ± .30
C, %	36 ± 7.4	41 ± 2.4	36 ± 7.0
N, %	1.34 ± .88	1.24 ± .45	1.41 ± .51
NH ₄ , μ g/g	196 ± 226.3	103 ± 63.5	138 ± 142
NO ₃ , μ g/g	4 ± 1.4	7 ± 3.2	6 ± 8.6
C/N	32 ± 15.6	36 ± 10.8	28 ± 7.3
P, %	.075 ± .033	.080 ± .017	.093 ± .031
PO ₄ , μ g/g	27 ± 9.3	35 ± 18.0	27 ± 15.8
Ca, %	1.4 ± 0.2	2.3 ± 0.6	2.4 ± 0.6
K, %	.05 ± .03	.04 ± .01	.03 ± .01
CEC, meq/100g	81 ± 10.9	137 ± 35.8	138 ± 32.2
TEC, "	126 ± 3.7	163 ± 38.0	160 ± 32.
base sat.	64 ± 10.5	84 ± 9.2	86 ± 8.6
depth, cm	80 ± -	84 ± 31.5	43 ± 18.3
tree species, basal area m ² /ha:			
b1. spruce	3.7 ± 6.7	10.9 ± 4.0	16.2 ± 2.1
tamarack	0.6 ± 0.2		0.5 ± 1.2

11111 1	1	1111111	11 111	11111	1	11	1	222561255523454 124
23312818997899378889917702112011902901277789900122	1244	3348812112	1334514833	222561255523454 124				
9012829946250129013238466634495258580023788791361759901434788677314917015316435724755061471869006803								
POPA	---	---	---	---	---	---	---	---
CAPA	---	---	---	---	---	---	---	---
brps	---	---	---	---	---	---	---	---
cani	---	---	---	---	---	---	---	---
AGSC	---	---	---	---	---	---	---	---
CXDD	---	---	---	---	---	---	---	---
capo	---	---	---	---	---	---	---	---
drad	---	---	---	---	---	---	---	---
ANPO	---	---	---	---	---	---	---	---
METR	---	---	---	---	---	---	---	---
TRMA	---	---	---	---	---	---	---	---
drve	---	---	---	---	---	---	---	---

11	1	1
1 3600 561266677155603466724560		
6896452905523701386424289537217		

CXCA	---	---	---	---	---	---	---	---
PEPA	---	---	---	---	---	---	---	---
thre	---	---	---	---	---	---	---	---
EQSC	---	---	---	---	---	---	---	---
PEVI	---	---	---	---	---	---	---	---
ROAC	---	---	---	---	---	---	---	---
heb1	---	---	---	---	---	---	---	---
cecu	---	---	---	---	---	---	---	---
clcs	---	---	---	---	---	---	---	---
clmu	---	---	---	---	---	---	---	---
ACMI	---	---	---	---	---	---	---	---
ASSP	---	---	---	---	---	---	---	---
CXTE	---	---	---	---	---	---	---	---
FRVI	---	---	---	---	---	---	---	---
GATR	---	---	---	---	---	---	---	---
LASP	---	---	---	---	---	---	---	---
LIBO	---	---	---	---	---	---	---	---
MEPA	---	---	---	---	---	---	---	---
RUPU	---	---	---	---	---	---	---	---
TREU	---	---	---	---	---	---	---	---
VIPA	---	---	---	---	---	---	---	---
eupu	---	---	---	---	---	---	---	---
JUBA	---	---	---	---	---	---	---	---
ORRO	---	---	---	---	---	---	---	---
COCA	---	---	---	---	---	---	---	---
dipo	---	---	---	---	---	---	---	---
hysp	---	---	---	---	---	---	---	---
CXPA	---	---	---	---	---	---	---	---

List of species in the TWINSpan-matrix (in order of appearance). The indicator species denoted by '*'.

I. Vascular plants

- **Carex capillaris* L.
- Petasites palmatus* (Ait.) A. Gray
- **Equisetum scirpoides* Michx.
- Petasites vitifolius* Greene
- Rosa acicularis* Lindl.
- Achillea millefolium* L.
- Aster* spp.
- Carex tenuiflora* Wahlenb.
- Fragaria virginiana* Duchesne
- Galium trifidum* L.
- Lathyrus* spp.
- **Linnaea borealis* L.
- Mertensia paniculata* (Ait.) G. Don.
- Rubus pubescens* Raf.
- Trientalis europaea* L.
- Viola palustris* L.
- Juncus balticus* Willd.
- Orchis rotundifolia* Banks ex Pursh
- Cornus canadensis* L.
- Carex paupercula* Michx.
- Epilobium* spp.
- Lonicera villosa* (Michx) T. & G.
- Senecio* spp.
- Petasites sagittatus* (Pursh) A. Gray
- **Equisetum sylvaticum* L.
- Ranunculus lapponicus* L.
- **Vaccinium vitis-idaea* L.
- Equisetum pratense* Ehrh.
- Gaultheria hispida* (L.) Bigel.
- Rubus chamaemorus* L.
- Empetrum nigrum* L.
- Eriophorum vaginatum* L.
- **Ledum groenlandicum* Oeder

II. Bryophytes

- Thuidium recognitum* (Hedw.) Lindb.
- Helodium blandowii* (Web. & Mohr) Warnst.
- Cetraria cucullata* (Bell.) Ach.
- Cladonia crispata* (Ach.) Flot.
- Cladonia multiformis* Merr.
- Eurhynchium pulchellum* (Hedw.) Jenn.
- Dicranum polysetum* Sw.
- **Hylocomium splendens* (Hedw.) BSG
- Dicranum undulatum* Brid.
- Peltigera aphtosa* (L.) Willd.
- **Pleurozium schreberi* (Brid.) Mitt.
- Cladina rangiferina* (L.) Harm.
- Drepanocladus exannulatus* (BSG) Warnst.
- Meesia triquetra* (L. ex Richt.) Angstr.
- Mylia anomala* S. F. Gray
- **Sphagnum fuscum* (Schimp.) Klinggr.
- Cladonia chlorophaea* (Flk.) Spreng.
- Cladonia cornuta* (L.) Hoffm.
- Cladonia cristatella* Tuck.
- Cladonia deformis* (L.) Hoffm.
- Cladonia mitis* (Sandst.) Hale & Culb.
- **Polytrichum strictum* Brid.
- **Sphagnum nemoreum* Scop.
- Ptilium crista-castrensis* (Hedw.) De Not.
- **Sphagnum angustifolium* (Russ.) C. Jens.
- **Tomenthypnum nitens* (Hedw.) Loeske
- Hypnum lindbergii* Mitt.
- Campylium chrysophyllum* (Brid.) J. Lange
- Campylium stellatum* (Hedw.) C. Jens.
- Climacium dendroides* (Hedw.) Web. & Mohr
- Hypnum pratense* Koch ex Spruce
- **Aulacomnium palustre* (Hedw.) Schwaegr.

- Pyrola secunda* L. (*Orthilia* s. L.)
Drosera rotundifolia L.
Smilacina trifolia (L.) Desf.
Vaccinium oxycoccos L.
Picea mariana (Mill.) Bsp.
Salix spp.
Pyrola asarifolia Michx.
Ribes spp.
Rubus acaulis (Michx.) Focke
Picea glauca (Moench) Voss
Carex gynocrates Wormsk.
Mitella nuda L.
Carex disperma Dewey
Galium boreale L.
Calamagrostis spp.
Equisetum arvense L.
Vaccinium myrtilloides Michx.
Carex aquatilis Wahlenb.
Betula pumila L.
Carex chondorrhiza L. f.
Stellaria crassifolia Ehrh.
Larix laricina (Du Roi) K. Koch
Carex limosa L.
Potentilla palustris (L.) Scop.
Caltha palustris L.
Agrostis scabra Willd.
Carex diandra Schrank
Andromeda polifolia L.
Menyanthes trifoliata L.
Triglochin maritima L.
- Sphagnum squarrosum* Crome
Sphagnum teres (Schimp.) Angstr. ex Hartm.
Sphagnum warnstorffii Russ.
Drepanocladus uncinatus (Hedw.) Warnst.
Sphagnum magellanicum Brid.
**Calliergon giganteum* (Schimp.) Kindb.
**Brachythecium turgidum* (C. J. Hartm.) Kindb.
Calliergon stramineum (Brid.) Kindb.
Drepanocladus fluitans (Hedw.) Warnst.
**Plagiomnium ellipticum* (Brid.) Kop.
Rhizomnium spp.
Sphagnum russowii Warnst.
Bryum pseudotriquetrum (Hedw.) Gaertn. et al.
Catoscopium nigrum Brid.
Campylium polygamum (BSG) C. Jens.
**Drepanocladus aduncus* (Hedw.) Warnst.
**Drepanocladus vernicosus* (Lindb. ex C. J. Hartm.) Warnst.

1. Nomenclature for vascular plants: Moss and Packer (1983)
 mosses: see sources in Vitt et al. (1975)
 lichens: Hale (1979)

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